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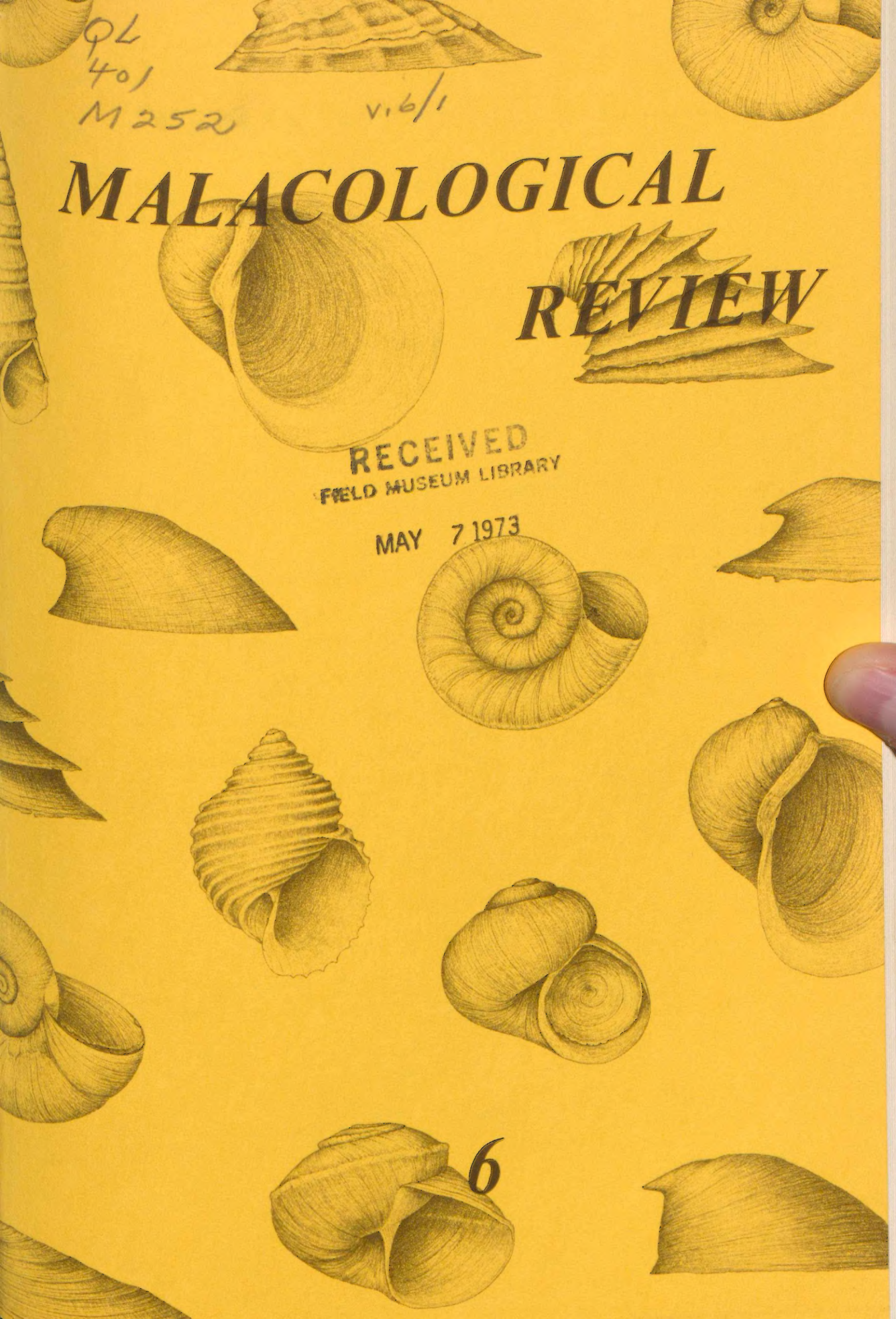

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ON THE COVER - Freshwater gastropod mollusks of the Lake Ohrid region, Macedonia, Yugoslavia. Illustrations by Carole W. Christman.

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Vol. 1: Succineidae (amber shells)
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Vol. 3: Epitoniidae (wentletraps)
Vol. 4: Conidae (cone shells)
Vol. 5: *Dysnomia* (freshwater mussels)
Vol. 6: Freshwater gastropods of the Lake Ohrid region, Yugoslavia

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Malacological Review, 1973, 6: 1-12

THE AMOEBOCYTES OF LAMELLIBRANCH MOLLUSCS, WITH SPECIAL REFERENCE TO THE CIRCULATING AMOEBOCYTES

Arun Shanker Narain

ABSTRACT

The phagocytic amoebocytes, found wandering freely within the body fluids and tissues of lamellibranchs, are widely involved in the functioning of the body.

The total number of circulating amoebocytes of lamellibranchs is very small in comparison to that of vertebrates. The total counts exhibit appreciable variation from individual to individual and even within an individual. A relationship between the feeding state and excretory activity of the lamellibranchs and the population density of their circulating amoebocytes appears to be very likely.

A common scheme of nomenclature and classification of the circulating amoebocytes of lamellibranchs is not available, although 2 schemes may be broadly made out. Nature of cytoplasmic granulation, staining property of cytoplasm, cellular size and its relative proportion to nuclear size have been commonly used as taxonomic parameters; but corpuscular movement, clumping and extension of protoplasmic processes also appear to be significant. It is further suggested that the system of nomenclature and classification of vertebrate leucocytes may also be partly made use of in connection with lamellibranch amoebocytes.

The amoebocytes of lamellibranchs extend protoplasmic processes for locomotion, clumping and phagocytosis. It appears that a sharp structural and nomenclative distinction between functionally different processes is likely to be more elucidating.

The circulating amoebocytes of lamellibranchs entangle by means of their protoplasmic extensions to form clumps. Clumping differs from vertebrate blood cell clotting in being reversible and without any accompanying fibrin formation, but its contribution in wound healing is essentially the same. It appears that friction and mechanical disturbances may serve as causative factors and that some sort of stimulus-response relationship may also exist between haemorrhage and clumping.

The amoebocytes of lamellibranchs ingest, digest and subsequently transport food material; segregate and excrete waste and harmful material; ingest and degrade infectious microbes; and mobilise and transport carbonaceous shell material. Phagocytosis and enzymatic activity of the amoebocytes play a very major role in the discharge of these functions.

Nothing definite is known about hemopoiesis in lamellibranchs.

In vitro cultivation of lamellibranch amoebocytes, with evident advantages, is being undertaken more frequently and opens the scope for diverse cell-interaction studies.

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INTRODUCTION

The amoebocytic corpuscles of invertebrates, particularly molluscs, have attracted much attention since Jones (1846) gave the first account of an invertebrate leucocyte. Study of the amoebocytes, found abundantly in molluscan body fluids, assumes special significance, since these cells are diversely involved to an appreciable extent in the functioning of the molluscan body.

Willmer (1945) has enumerated 3 major characteristics of an amoebocyte, namely, ability to move independently with the aid of pseudopodia, marked tendency of phagocytosis and wandering nature. Hence, amoebocytes found in one part of the body at one time are likely to be found in other parts at other times. Evidently, therefore, it may not always be possible to draw a sharp line of demarcation between the circulating amoebocytes and other amoebocytes.

Since Ryder (1882) observed amoeboid movement in oyster amoebocytes, Haeckel (1862) demonstrated phagocytosis in *Helix* and *Thetis* amoebocytes, and Lankester (1885) found oyster amoebocytes wandering freely on the gill surface, extensive studies have been carried out on these lines; and the aforesaid 3 properties of molluscan amoebocytes are now fairly well established (Takatsuki, 1934; Wagge, 1955; Franc, 1960; Hill & Welsh, 1966).

Functional importance of phagocytosis by molluscan amoebocytes can be twofold. Firstly, they can assist in digestion and subsequent absorption by ingesting food matter, digesting it intracellularly and carrying the digested products to the tissues. Secondly, they can help in excretion by ingesting waste and harmful matter and carrying it to the exterior or to the excretory channels of the body. In either case, these cells necessarily have to move about from place to place; hence, their amoeboid and wandering properties assume the status of behavioural necessities for an efficient carrying out of the aforesaid functions.

TOTAL NUMBER OF AMOEBOCYTES

The available reports (Dundee, 1953: *Amblema costata, Anodonta grandis, Lampsilis fallaciosa, Ligumia subrostrata, Quadrula quadrula, Tritogonia verrucosa, Uniomerus tetralasmus;* Fingerman, Fairbanks & Plauche, 1957: *Crassostrea virginica;* Tanaka & Takasugi, 1964a: *Anadara subcrenata;* Feng, 1965a: *Crassostrea virginica;* Narain, 1972a: *Lamellidens corrianus*)reveal that the number of amoebocytes, in fact the total number of cells, present within the blood of lamellibranchs is extremely small in comparison to that in vertebrate blood and varies appreciably in samples drawn from different individuals or from the same individual at different times.

Although no general explanation is available for the fluctuation of total blood cell counts, a few hypotheses have been put forth. Dundee (1953) has suggested that, in the different unionids studied by her, the number of blood cells is likely to fluctuate during blood extraction, since these mussels shed their blood cells under abnormal conditions. Feng (1965a) has made interesting observations regarding the fluctuation of blood cell counts in *Crassostrea virginica*. He has propounded that while the number of blood cells within an individual is dependent on the intensity of agitation of blood by cardiac beating, it may vary from individual to individual, since the blood cells partake actively in the nutrition, and since all the individuals are not likely to be at the same stage of feeding. The probability of the presence of a similar relationship of cardiac rhythm and feeding state of the individuals with the fluctuation of total blood cell numbers has also been suggested for *Lamellidens corrianus* (Narain, 1972a).

The contentions of Feng (1965a) appear to be basically quite logical; particularly, the interrelationship of feeding activity of individuals and their blood amoebocyte numbers can be of a general application. Lamellibranch amoebocytes in general are definitely known to wander about for the ingestion of food particles in the gut region and for the subsequent transport of nutritive material. The presence or absence of a particular amoebocyte in the blood stream would evidently depend on its wandering activity, which in turn would depend on the nutritive activity of the animal. The population density of blood amoebocytes would, therefore, be determined by the stage of the animals' feeding and is hence likely to show individual variation. By a similar logic, the amoebocyte population of lamellibranch blood would also appear to be dependent on the excretory activity of the animals, since the amoebocytes are also definitely known (Potts, 1967) to wander through the body of lamellibranchs for carrying the undesirable matter to excretory channels.

NOMENCLATURE AND CLASSIFICATION

The first attempt to classify the circulating amoebocytes of lamellibranchs into different types seems to have been made by DeBruyne (1896), who described 7 blood cell types in *Anodonta cygnea*, *Mytilus edulis*, *Ostrea edulis* and *Unio pictorum*. Since then, several types of amoebocytes have been described in the blood of various lamellibranchs (Takatsuki, 1934; Wagge, 1955; Hill & Welsh, 1966), but no common scheme for their nomenclature and classification seems to have been evolved. However, broadly speaking, 2 main patterns of classification of these cells may be made out.

In 1 pattern of classification, the amoebocytes are divided into 2 categories: (a) hyaline corpuscles or lymphocytes, having a homogeneous cytoplasm with only a few, if any, granules; and (b) granulocytes, having a granular cytoplasm which is full of granules that vary greatly in shape, size and staining reactions. This scheme has been followed by Takatsuki (1934) for *Ostrea edulis* and by Ohuye (1937, 1938a, b) for *Anomia liscki*, *Arca inflata*, *Glycymeris vestitus*, *Libitina japonica*, *Mytilus edulis* and *Ostrea circumpicta*. The lymphocytes of *Ostrea edulis* (Takatsuki, 1934) are 5-15 μ in diameter and sometimes contain a few granules, whereas those of *Arca inflata* (Ohuye, 1937) are either small (4-6 μ diameter) with no cytoplasmic granules or large (8-12 μ diameter) with a few rounded basophilic cytoplasmic granules. The granulocytes, on the other hand, present a larger variety. The granulocytes of *Ostrea edulis* (Takatsuki, 1934) are 9-13 μ in diameter, have a nucleus of 3-4 μ diameter and possess neutrophilic granules that show a basophilic tendency. The granulocytes of *Arca inflata* (Ohuye, 1937), *Anomia liscki*, *Libitina japonica*, *Mytilus edulis* and *Ostrea circumpicta* (Ohuye, 1938a) are also of 1 type, the granules being acidophilic in the case of *Anomia liscki* and neutrophilic with basophilic tendency in the rest of the lamellibranchs. The granulocytes of *Glycymeris vestitus* (Ohuye, 1937) are, however, of 2 types: finely granular and coarsely granular. In the opinion of Ohuye (1938b), lymphocytes are the stem cells from which other types originate.

The other scheme of classification was first introduced by Cuénot (1891), who divided invertebrate leucocytes into 3 main types: (a) finely granular corpuscles; (b) coarsely granular corpuscles; and (c) corpuscles with very little cytoplasm around the nucleus. This scheme has been elaborated and modified by later workers. Drew (1910), while retaining this nomenclature for the amoebocytic blood cells of *Cardium norvegicum*, has also taken into consideration the acidophilic and basophilic properties of these cells. Thus, 48% of the amoebocytes of

the blood of this lamellibranch are finely granular with eosinophilic granules, 44% are coarsely granular with eosinophilic granules, and 8% are small cells with a very thin layer of basophilic cytoplasm around the nucleus. Dundee (1953), working with *Amblema costata*, *Anodonta grandis*, *Carunculina parva*, *Lampsilis fallaciosa*, *Lasmigona complanata*, *Leptodea fragilis*, *Ligumia subrostrata*, *Proptera alata*, *Quadrula quadrula*, *Tritogonia verrucosa* and *Uniomerus tetralasmus*, further elaborated the scheme and also considered the diameter of the blood cells possessed by their nuclei. She also modified the nomenclature and divided the amoebocytic blood cells of these mussels into: (a) granular eosinophilic amoebocytes, representing 85% of the total, being 8-20 μ in diameter, having a granular acidophilic cytoplasm and possessing an ovoid eccentric nucleus that occupies 1/3 of the diameter of the cell; (b) granular basophilic amoebocytes, representing 7% of the total, being 7-12 μ in diameter, having a granular basophilic cytoplasm with occasional red granules and possessing a nucleus that occupies 1/3-1/2 of the diameter of the cell; and (c) macronucleocytes, representing 7.5% of the total, being 10-20 μ in diameter, having a finely granular cytoplasm with scattered red granules and possessing a large nucleus that occupies 1/2-2/3 of the diameter of the cell. Cuénot (1891) considered the coarsely granular corpuscles to be the original form whose degeneration gives rise to the other 2 types, but Drew (1910) has expressed disagreement with this view.

Many workers have not classified the amoebocytic blood cells of lamellibranchs into types but have simply mentioned some characteristics of a single type of cell. Thus, *Anodonta*, *Solen* and *Unio* have acidophilic and *Pectunclus* neutrophilic granules within their amoebocytes (Knoll, 1893); the oyster has amoebocytes of 10 μ (Herdman & Boyce, 1899) or 1/300 inch (Ryder, 1882) diameter which contain fragmented nuclei (Carazzi, 1896) and green or other coloured granules (Carazzi, 1896; Herdman & Boyce, 1899); *Pecten* has spherical amoebocytes with prominent nuclei (Dakin, 1909); *Anadara inflata* has finely granular amoebocytes of 8 μ diameter (Sato, 1931); *Actinonaias carinata*, *Amblema peruviana*, *Elliptio crassidens*, *Fusconaia ebena*, *Lampsilis purpurata*, *Lasmigona complanata*, *Megalonaias gigantea* and *Tritogonia verrucosa* have amoebocytes that are 5-25 μ in diameter and have dark staining eccentric nuclei and coarsely granular eosinophilic cytoplasm (Motley, 1933); *Mytilus* possesses amoebocytes which are completely filled with granules (White, 1937); and *Venus mercenaria* has granular amoebocytes that have a diameter of 9-12 μ (Zacks, 1955). Mention of some structural features of amoebocytes has also been made in reports on the oyster amoebocytes emerging from *in vitro* cultivated tissue explants (Orton, 1922; Kenny, 1964; Perkins & Menzel, 1964; Li, Stewart & Drinnan, 1966; Tripp, Bisignani & Kenny, 1966). Evidently, descriptions like these are far from being very complete. On the other hand, an extreme amount of detail is made available in the description and classification of the amoebocytes of the blood of *Gryphea gigas* and *Anadara subcrenata* given by Tanaka, Takasugi & Maoka (1961) and Tanaka & Takasugi (1964b) respectively. These authors have considered many more parameters (viz., shape and size of the cell and the nucleus; position and colour of the nucleus; state of the chromatin, the nuclear membrane and the nucleoli within the nucleus; nature of the cytoplasmic granules; and nature of the perinuclear zone) and have distinguished as many as 6 major types of cells (I-R large, I-R medium, I-R small, I-S, II large, II small, III large, III small, IV, V large, V medium, V small and VI), which fall under 2 broad categories, i.e., granulocytic and agranulocytic types.

The parameters taken into account by the different aforesaid workers, particularly the nature of cytoplasmic granulation, the staining property of cytoplasm,

the size of the cells and the relative proportion of the cellular and nuclear sizes, are undoubtedly significant. But it seems that corpuscular behaviour with regard to movement, clumping and protoplasmic extensions, which has been found significant in lamellibranchs like *Lamellidens corrianus* (Narain, 1972a), may also be considered as a general taxonomic parameter. Moreover, a restricted use of the well established scheme for vertebrate leucocytes may be helpful in providing more clarity and uniformity in the description of lamellibranch blood amoebocytes also. These considerations form the basis of the nomenclature and classification system adopted in the case of lamellibranchs like *Lamellidens corrianus* (Narain, 1968, 1972a). The amoebocytic blood cells of this mussel have been categorised into 3 types: (a) acidophils, which are the largest, have a coarsely granular acidophilic cytoplasm occupying approximately 8/9 of the cell, move with moderate speed, extend a moderate number of filipodia, participate less actively in clumping and constitute 26.32% of the total; (b) large basophils, which are smaller, have a finely granular basophilic cytoplasm occupying approximately 3/4 of the cell, move the slowest, extend the maximum number of filipodia, participate most actively in clumping and constitute 60.20% of the total; and (c) small basophils, which are the smallest, have a finely granular basophilic cytoplasm occupying approximately 1/4 of the cell, move the fastest, extend filipodia very rarely, participate very passively in clumping and constitute 13.48% of the total (Fig. 1).

MOVEMENT AND PROTOPLASMIC PROCESSES

All the reports on the movement of amoebocytes of molluscs, including lamellibranchs, almost invariably refer to an amoeboid motion. However, Griesbach (1891) stated that there are differences between the movement of molluscan amoebocytes and that of *Amoeba;* and Haughton (1934) was of the opinion that the pseudopodic extensions of invertebrate blood cells are not always true pseudopodia but are often merely a thigmotactic flowing of protoplasm. Nevertheless, there appears to be little doubt about the amoeboid nature of the movement of molluscan amoebocytes in general.

The protoplasmic extensions of the amoebocytic blood corpuscles of lamellibranchs have attracted the attention of many workers. Dakin (1909) has observed fine bristle-like and often branched pseudopodia bringing about locomotion and clumping of the amoebocytes of *Pecten.* Drew (1910) has found the amoebocytes of *Cardium norvegicum* extending very long and slender pseudopodia which help these cells in phagocytosis and clumping. Zacks (1955) has mentioned spike-like pseudopodia helping in the movement of the amoebocytes of *Venus mercenaria.* Bang (1961) has seen filamentous pseudopodia which bring about the movement of the amoebocytes of *Crassostrea virginica.*

It is evident from such reports that the amoebocytes of the blood of lamellibranchs put out protoplasmic processes for locomotion, clumping and phagocytosis. But the reports do not clearly indicate whether the protoplasmic processes extended for the different corpuscular activities are of 1 type or of different types; and if the latter be the case, then the use of a common term, 'pseudopodia', does not seem to be entirely justified. It would appear that a sharper distinction between the protoplasmic processes serving different corpuscular functions is more desirable and that a nomenclature of these processes based on their function is likely to be more elucidating. Takatsuki's (1934) observation that small lamellate processes bring about movement while filamentous bristle-like processes bring about clumping of *Ostrea edulis* amoebocytes provides a certain amount of

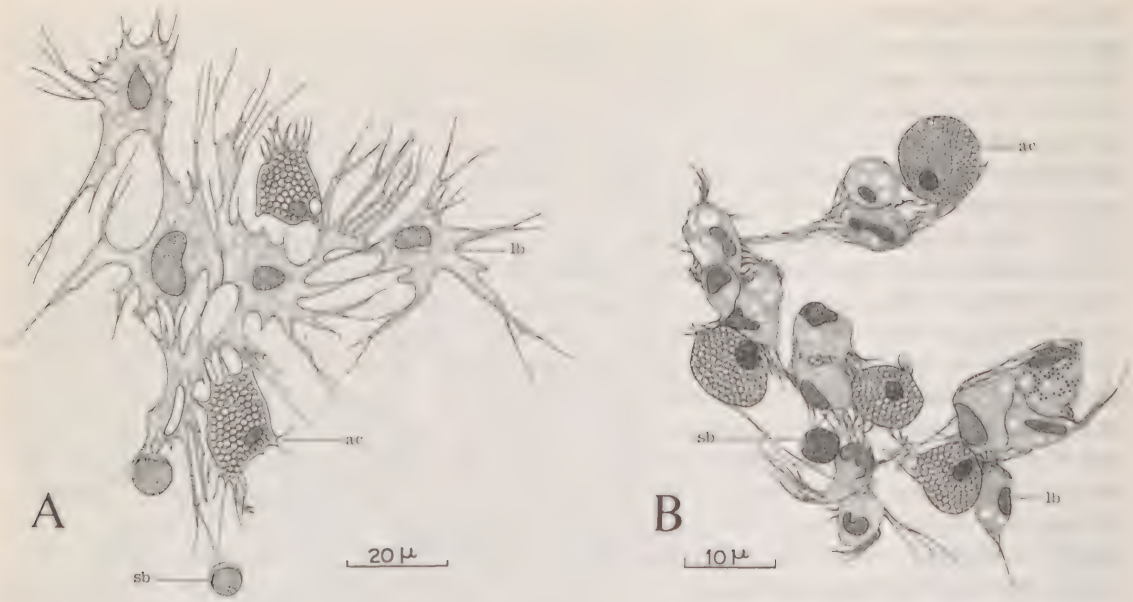

FIG. 1. Circulating amoebocytes of *Lamellidens corrianus* (after Narain, 1969). A, Living preparation; B, Formol vapour fixed preparation. ac, acidophil; lb, large basophil; sb, small basophil.

distinction between the functionally different structures. However, this author has not only chosen to call both these types of processes 'pseudopodia' but has also expressed agreement with Goodrich's (1919) view that the filamentous processes are actually either optical sections of lamellate pseudopodia or are products of abnormal environmental conditions. The reports on the protoplasmic processes of the amoebocytic blood cells of *Amblema costata*, *Anodonta grandis*, *Carunculina parva*, *Lampsilis fallaciosa*, *Lasmigona complanata*, *Leptodea fragilis*, *Ligumia subrostrata*, *Proptera alata*, *Quadrula quadrula*, *Tritogonia verrucosa*, *Uniomerus tetralasmus* (Dundee, 1953) and *Lamellidens corrianus* (Narain, 1972a) seemingly present a much more clearly specified distinction between the functionally different types of processes. In these cases, the separate identities of 2 kinds of processes have been completely established. The broad and lamellate processes, which are concerned with corpuscular movement, have been called 'pseudopodia,' while the delicate processes, which are concerned with interconnection and clumping of the amoebocytes, have been called 'spinous processes' (Dundee, 1953) or 'filipodia' (Narain, 1972a). There seems to be justification in Franc's (1960) statement that although both petaloid and filamentous protoplasmic processes may exist together and at the same time in lamellibranch amoebocytes, yet their functions are not the same.

CLUMPING REACTION

As early as 1880, Geddes observed that the perivisceral fluid of different invertebrates, including the lamellibranch *Mytilus*, soon separated into 2 parts superficially akin to clot and serum of vertebrate blood. He propounded that the 'clots' are formed partly or wholly by the fusion of amoebocytes into homogeneous masses, which he called 'plasmodia.' However, Michel showed in 1888 that the congregating cells did not lose their identity but merely got attached by

their hyaline ectoplasmic layers and remained capable of resuming their independence. Observations made since then on the clumping of the circulating amoebocytes of a variety of invertebrates have largely upheld Michel's contention.

It is now well established that the amoebocytic elements of the blood of lamellibranchs tend to aggregate into clumps by getting held together through their protoplasmic extensions, though minor variations have been observed in the actual process of clump formation in different forms. The amoebocytes of the blood of *Cardium norvegicum* establish contact by their pseudopodia, and the interconnecting bridges so formed then shorten, thicken and contract to bring the attached cells together (Drew, 1910); those of *Amblema costata*, *Anodonta grandis*, *Carunculina parva*, *Lampsilis fallaciosa*, *Lasmigona complanata*, *Leptodea fragilis*, *Ligumia subrostrata*, *Proptera alata*, *Quadrula quadrula*, *Tritogonia verrucosa* and *Uniomerus tetralasmus* bump into each other with their spinous processes to subsequently form a mass (Dundee, 1953); while those of *Lamellidens corrianus* (Fig. 1) get entangled by their filipodia and are eventually pulled together (Narain, 1972a).

Clumping of the amoebocytic blood corpuscles of lamellibranchs is basically different from blood clotting of vertebrates. Firstly, there is no involvement of plasma in the process of clumping. Formation of any fibrous elements within the blood plasma of lamellibranchs has not yet been observed, with the only probable exception of certain 'extracellular clots' observed by Bang (1961) in *Crassostrea virginica*. The absence of a fibrinogen-thrombin-fibrin system has actually been confirmed by biochemical tests in lamellibranchs like *Lamellidens corrianus* (Narain, 1972b). Secondly, there is no permanent fusion of the clumped cells. The process of clumping is reversible, and the congregating cells remain capable of dissociating from the clumps. The term 'clotting' would, evidently, be a misnomer for the massing together of the amoebocytes of the blood of lamellibranchs.

Formation of a clot, as an initial step in wound healing, is an important function of vertebrate blood. Lamellibranch blood cells and their clumps also are known to delineate and plug wounds and check haemorrhage (Dakin, 1909; Drew, 1910; Goodrich, 1919; Orton, 1923; Bang, 1961; Desvoigne & Sparks, 1968, 1969). Moreover, it is seen that during injury or infection there is a rapid infiltration of blood amoebocytes towards the affected area, where these cells clump and plug the wound or surround the infected region to isolate it, while the free phagocytes repair the damaged part or remove the infecting organism (Drew & DeMorgan, 1910; Wagge, 1955; Mackin, 1961; Beedham, 1965; Desvoigne & Sparks, 1968). While these observations furnish a direct evidence of the functional significance of the clumping reaction of lamellibranch blood cells, an indirect evidence may also be provided by the relative abundance in lamellibranchs like *Lamellidens corrianus* of those blood cell types which are more capable of active clumping (Narain, 1972a). Hence, there appears to be much truth in the statement of Drew & DeMorgan (1910) that although the manner of clotting in lamellibranchs differs markedly from that of vertebrates, such a reaction to injury of tissue is essentially similar. However, George & Ferguson (1950) consider such a plugging of wounds by blood cell clumps as an ineffective haemostatic mechanism, which is accidental and of no survival significance to the animals. Nevertheless, there appears to be practically no doubt regarding the importance of the phenomenon of blood cell clumping in the survival of lamellibranchs.

A few attempts have been made to investigate the causative factors of blood cell clumping in lamellibranchs. The studies made in this connection on lamelli-

branchs like *Cardium norvegicum* (Drew, 1910) and *Lamellidens corrianus* (Narain, 1972a) suggest that contact and friction with foreign objects and mechanical agitation may act as promoting causes for blood cell clumping and that haemorrhage may impart the power of amassing to the amoebocytic blood elements. However, much work appears to be needed on these lines to understand the regulating factors for this fascinating behaviour of lamellibranch blood cells.

DIGESTIVE FUNCTION

The importance of amoebocytes in the digestive process of molluscs, particularly lamellibranchs, is well known, and the voluminous literature on intracellular digestion within these cells is covered effectively by the reviews of Takatsuki (1934), Wagge (1955), Owen (1966) and Purchon (1968). Noteworthy in this connection are the views of Yonge (1937, 1946). He holds the firm opinion that the amoebocytes of lamellibranchs, being provided with a variety of digestive enzymes, are the major means of digestion and that they ingest food particles, digest them intracellularly and then transport the end-products to the tissues and blood. Yonge's views have been widely supported and may be considered as universally accepted (Wagge, 1955; Owen, 1966; Purchon, 1968). But workers like Mansour (1946a, b) and Mansour-Bek (1946a, b) do not agree totally with Yonge and consider extracellular digestion to be the major mode of digestion in lamellibranchs. Similarly, George (1952) challenges the contention of Yonge that the amoebocytes, laden with ingested material, migrate back to the tissues and blood. However, none of the critics of Yonge's views doubt the capacity of the amoebocytes to ingest, and subsequently digest, the larger particles.

The abundance of amoebocytes in the gut and digestive gland of practically all the lamellibranchs studied (Owen, 1966; Purchon, 1968) and the presence of various carbohydrate, protein and fat digesting enzymes within these cells (Yonge, 1926; Takatsuki, 1934; George, 1952; Zacks & Welsh, 1953; Zacks, 1955; Wagge, 1955; Janoff & Hawrylko, 1963; Feng, 1965b; Owen, 1966; Narain, 1972b) have been fairly well established. The evidence supporting the role of amoebocytes in the digestive process of lamellibranchs is overwhelming and would fully justify Owen's (1966) conclusions in this connection: "There seems little doubt that in lamellibranchs and many gastropods, amoebocytes transport, digest and release nutritive material within the tissues. It also seems clear that amoebocytes free in the lumen of the gut can and do ingest particles but whether they then migrate back into the tissues is doubtful."

Mention might be made here of the peculiar association of the amoebocytes of Tridacnidae and the alga *Zooxanthellae*, which, according to Yonge (1966), is of a symbiotic nature and probably assists the lamellibranchs in their nutrition and excretion. Harbouring of *Zooxanthellae* may be useful for lamellibranchs, since, as suggested by Goreau, Goreau, Yonge & Neumann (1970), the inorganic waste of the lamellibranch can be utilised by the alga, and the resultant increase in the algal component can be made available as food to the lamellibranch.

OTHER FUNCTIONS

Amoebocytes seem to have an important phagocytic role during excretion in molluscs, particularly in eliminating insoluble particles from the circulation. The wandering amoebocytes phagocytose the particles and migrate to the gut, the pericardium, the excretory organs or the mantle cavity; they either move out of the body through these viscera or return after releasing the particles (Wagge,

1955; Potts, 1967). Potts (1967) considers the evidence strong enough to permit an analogy of these cells with the reticulo-endothelial system of vertebrates.

Reports are available suggesting segregation and excretion of different harmful and waste substances by the amoebocytes of various lamellibranchs: degenerated pigments in *Anodonta* and *Unio* (Durham, 1891); oil globules in *Unio* (Canegallo, 1924); harmful metals (Orton, 1923), diseased and necrotic leucocytes (Sparks & Pauley, 1964), and injected melanin particles (Stauber, 1950), human red blood cells (Tripp, 1957) and thorotrast (Nakahara & Bevelander, 1969) in the oyster; and ceroid-like pigments in *Venus* (Zacks, 1955).

Strong reaction against parasitic infestation has also been mentioned in connection with molluscan amoebocytes (Tripp, 1963); and the amoebocytic blood cells of lamellibranchs like *Cardium norvegicum* (Drew, 1910) and the oyster (Stauber, 1950; Tripp, 1960, 1965; Mackin, 1961) have been observed ingesting and degrading infectious organisms like bacteria, fungi and Protozoa.

Special functions, like transport of calcium and protein from the digestive gland to the shell formation area, have also been assigned to molluscan amoebocytes (Wagge, 1955; Wilbur, 1964). Reports are available that the wandering amoebocytes of lamellibranchs are concerned with the transfer of shell material to the site of shell formation during repair of shell damage in lamellibranchs like *Mytilus edulis* (Dunachie, 1963) and *Anodonta* (Beedham, 1965). There are also indications that the phosphatase activity of these cells is somehow involved during the process of transfer and deposit of shell material; and while the amoebocytes of lamellibranchs like *Lamellidens corrianus* are known to possess alkaline phosphatase (Kamat, 1956), the phosphatase content of the blood of lamellibranchs like *Mytilus* has been shown to increase during shell regeneration (Manigault, 1939). However, the actual mechanism of the mobilisation of carbonaceous shell material by the amoebocytes of lamellibranchs, with the probable aid of their phosphatases, is not properly understood.

A role of amoebocytes in the absorption of iron has also been suggested in some cases. The amoebocytes of lamellibranchs like *Mytilus edulis* absorb ferritin, previously fixed by the branchial epithelium, and this is characterised by a high acid phosphatase activity (Pasteels, 1967).

HEMOPOIESIS

Nothing is definitely known as yet regarding the seat of formation of the amoeboctyes of molluscan blood. Cuénot (1891) suggested that these cells might be originating from special "glande lymphatiques" at the base of the gills. But not much attention seems to have been paid since then to hemopoiesis in molluscs, although a few opinions have been expressed (Hill & Welsh, 1966).

As regards the site of production of circulating amoebocytes of lamellibranchs, Tanaka (pers. comm., 1969) has expressed interesting views. He considers the digestive canal to be the centre of hemopoiesis in shellfish and suggests that the digestive products from the food, called "monreal" or "life-substances," may be utilised for blood cell production by the cilia of the intestinal wall. Morton (1969) has suggested that the circadian rhythm of adductor activity and quiescence may be related to the formation of at least part of the supply of the blood amoebocytes of *Dreissena polymorpha*. The issue of hemopoiesis is, however, still obscure, and there does not appear to be any convincing evidence to support the few hypotheses that have been put forth in this connection.

IN VITRO CULTURES OF AMOEBOCYTES

Studies on the cultures of lamellibranch amoebocytes are in a comparatively young stage, and most of the work has been done with oysters. Attempts have been made to cultivate oyster amoebocytes *in vitro* and to study their survival and behaviour, particularly their interaction with foreign objects like bacteria, fungi, protozoans and yeast (Orton, 1922; Mackin, 1961; Tripp, 1963; Kenny, 1964; Perkins & Menzel, 1964; Tripp, 1965; Tripp, *et al.*, 1966; Li, *et al.*, 1966). Such studies not only furnish better opportunities for investigating the diverse behaviour of the amoebocytes of lamellibranchs but also provide a good means for the study of different pathogens. Shellfish amoebocyte cultures can serve as useful tools for observing the fate of different intracellular microbes and for establishing the relationship of the lamellibranchs to their own and to human and other pathogens. The scope can thus be opened for a better understanding of the pathogenecity of various pathogens and for identifying and isolating shellfish pathogens.

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ADDENDUM

The earlier mentioned nomenclature and classification scheme followed by Takatsuki and Ohuye has also been adopted in the case of *Tapes semidecussata*[1] in which 2 types of formed elements, i.e., hyaline leucocytes and granular leucocytes, with cellular and nuclear diameters of 1.6-16 μ and 1.5-7 μ respectively, have been described. Moreover, this clam falls in line with other lamellibranchs in having low and fluctuating leucocyte counts.

[1]CHENEY, D. P. 1971. A summary of invertebrate leucocyte morphology with emphasis on blood elements of Manila clam, *Tapes semidecussata*. *Biol. Bull.*, 140(3): 353-368.

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INTERNAL DEFENSE MECHANISMS OF *OCTOPUS DOFLEINI*[1]

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ABSTRACT

Octopi were injected with living bacteria or colloidal carbon and the clearance rates and sites studied. Like other molluscs, the octopus clears particles from its blood rapidly and may do this in specialized tissues rather than by means of blood phagocytes. Later innoculations of bacteria are cleared no more rapidly than primary ones, and no humoral antibacterial agent could be found in octopus blood, even if the octopus had previously encountered the bacterium. For clearance to occur, the blood must be circulating.

INTRODUCTION

Perhaps the most economically important areas of molluscan biology are (1) food from oysters and (2) trematode transmission by snails. It is not, therefore, entirely surprising to find that the literature on molluscan internal defense mechanisms is limited to bivalves and gastropods (Bayne, 1972), except for a single paper on an octopus (Stuart, 1968). It has been found that in these 2 widely studied groups, defense depends upon the hemolymph, particularly upon the activities of hemocytes - the amebocytic "blood cells" (Tripp, 1970). There have been scattered reports of bacterial lysins in molluscan body fluids (McDade & Tripp, 1967), but, despite extensive efforts, only one report of an humoral bacterial immunity has been published (Cushing, Evans & Evans, 1971).

In view of the higher level of physiological complexity of the cephalopods, I considered (Bayne & Kime, 1970) that it would be valuable to study their internal defense mechanisms. It seemed at least possible that they might have a more complex or refined response to injected particles than are the responses of bivalves and gastropods. I therefore investigated these responses in the giant octopus of the northeastern Pacific, *Octopus dofleini*. The research was carried out at the University of Washington Friday Harbor Laboratories, during June and July, 1972.

RESEARCH

The experiments were designed to answer a series of questions. (1) Can an octopus clear live bacteria (*Serratia marcescens*) from its circulatory system? If it can, (2) How fast does it do this? (3) Does the octopus have an immune response? (4) Is phagocytosis by blood cells the mechanism used? (5) What is the site of removal (general or localized)?

In order to answer these questions, several procedures became routine.

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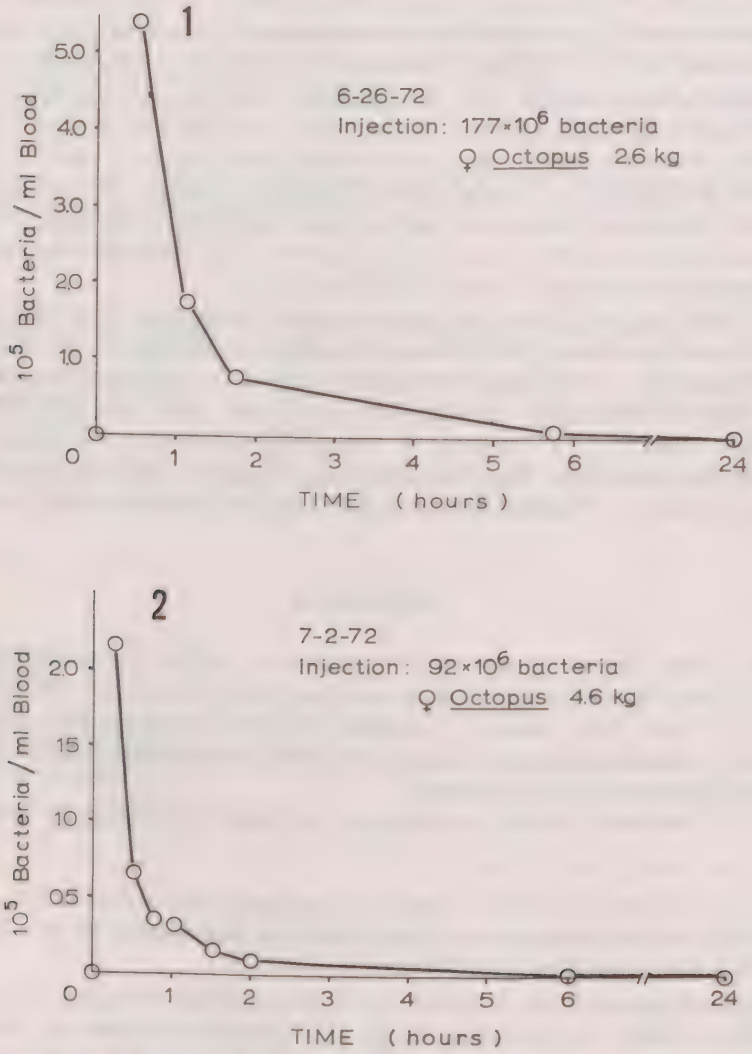
[2]Grateful acknowledgement is made to Dr. R. L. Fernald for provision of research facilities, and to David Alford and Berkeley Bayne for laboratory assistance. Karen Miller prepared the illustrations. The Oregon State University Travel Fund kindly helped with moving costs.

Briefly, the bacterium *Serratia marcescens* was chosen because it grows in characteristic red colonies, allowing one to readily distinguish it from other bacteria. It is non-marine, but survives in *Octopus* saline (LD 50 = 24 hrs.). The bacteria were grown at room temperature in nutrient broth and were routinely spun down (centrifuged), rinsed and resuspended in *Octopus dofleini* saline (Smith, 1962) prior to injection. Each octopus was anesthetized by placing it in 10 liters of sea water and adding ethanol drip-wise to a concentration of 2% over about 20 minutes; the octopus became relaxed within about 30 minutes and could be removed from the tank and have its gills partly extruded from the mantle cavity so that needles could be inserted into the large efferent branchial vein. Blood samples were taken prior to the injection and at various intervals after injection. To take blood, a syringe with a 26 gauge needle was inserted into the efferent branchial vein and blood carefully withdrawn. The blood was added to nutrient agar, serially diluted, and poured into petri plates where the bacteria were counted after at least 24 hours growth. Results of 2 typical clearance experiments are shown in Figs. 1 and 2.



FIGS. 1 and 2. Rates of clearance of *Serratia marcescens* from the blood of *Octopus dofleini*. Most of the injected bacteria are removed from the circulation within 2 hours.

These data provide answers to the first 2 questions. (1)Yes, bacteria are cleared from the circulation (or rendered nonviable); (2) Even under suboptimal conditions (drunk octopi do not circulate their blood as actively as do sober octopi), in about 2 hours the bacteria are 95% gone.

To answer the question of an immune response, 2 approaches were used. (a) An identical clearance experiment was carried out on an octopus which had received 4 bacterial injections (between 30 and 90 million per time) 24, 17, 9 and 5 days before. The clearance rate (Fig. 3) was unchanged, indicating that prior exposure to the bacteria had not led to an ability to increase the rate of clearance. (b) Blood was collected from an octopus which had been subjected to a series of injections 21, 14, 6 and 2 days previously; control blood was collected from a previously unchallenged octopus. The serum was collected into autoclaved test tubes by filtration through sterile 0.45 μ milipore filters. This serum (~2.5 ml) was inoculated with bacteria and maintained at the same temperature as the

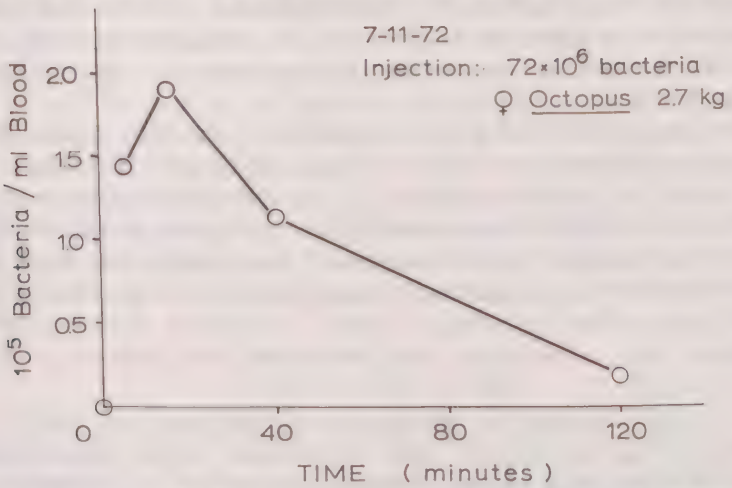


FIG. 3. Rate of clearance of *Serratia marcescens* from the blood of an *Octopus dofleini* which had received similar injections on 4 previous occasions. The clearance rate was no faster than that found in control octopi.

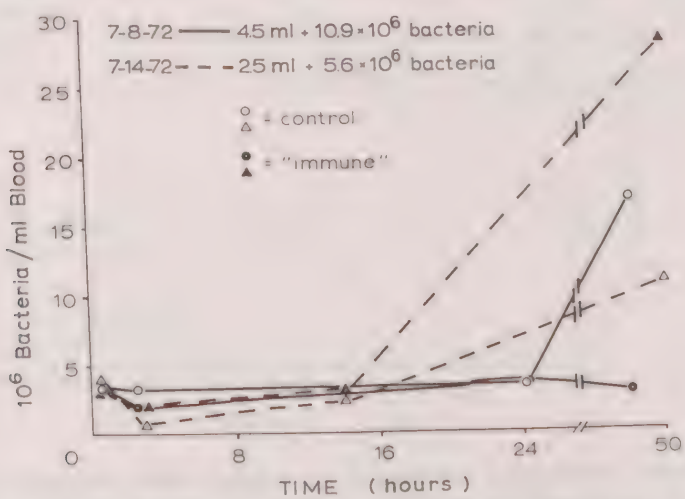


FIG. 4. Survival of *Serratia marcescens* in octopus serum. Bacteria survived in both control serum and serum from a previously injected octopus. No antibacterial effect is evident.

octopus (11 ± 1°C). Subsamples were taken periodically to see if there was any evidence of a bacteriocidal factor in the "immune serum"; any such factor would be evident from a decrease in bacterial numbers in that serum. The data are plotted in Fig. 4. Although these data are preliminary, and do not warrant any conclusive statement, they do at least suggest that no bacteriocide is present in either control or "immune" serum. No bacterial kill-offs occurred, and growth occurred in both sera.

So question 3 - Is there an immune response? - can be answered in part. Prior exposure to the bacteria does not enhance the clearance mechanisms. Neither is any humoral lysin or other anti-microbial factor evidently produced. A third possibility has not been investigated; this is the rate of elimination or kill-off of bacteria after clearance from the circulation.

Question 4 was "Is phagocytosis by blood cells the mechanism used for *in vivo* clearance?" Other work on snails (Bayne, 1973) suggests that this is not the mechanism in those molluscs. I furthermore believe that I have conclusive evidence that in the octopus the answer is no; phagocytosis by circulating blood cells is not responsible for clearance. One source of supporting evidence is the following experiment.

The afferent branchial artery of a live octopus was ligatured in 2 places to provide an isolated "island" of about 1.5-2 ml. of blood. A sample of blood (about 30 μl) was taken for determination of the number of bacteria. Then 740,000 bacteria in 40 μl of octopus serum were injected. Active peristalsis was observed throughout the duration of the experiment (indicating the live condition of the octopus). The area of the experimental "blood island" was maintained at 10-15°C by means of cool sea-water moistened paper. Samples of blood (30 μl each) were taken at several time intervals and processed for bacterial numbers. Fig. 5 illustrates the results.

Although a trend towards a reduction of bacteria is evident over the first hour, clearance is not achieved. The conditions in this experiment, except for the arrested blood flow, can be considered ideal for *in vivo* phagocytosis by blood cells, and the bacteria were present in a proportion similar to that occurring

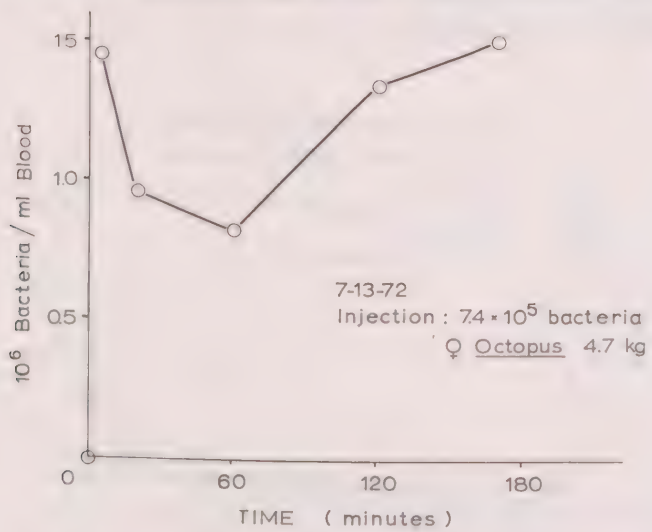


FIG. 5. The course of bacterial numbers in an isolated afferent branchial vein of *Octopus dofleini*. Differences between this and Figs. 1 and 2 illustrate a failure to achieve clearance in this experiment. Whether or not the initial drop in numbers was due to phagocytosis by blood cells is not apparent. Evidently blood clearance is not achieved unless the blood is circulating.

in earlier *in vivo* clearance experiments. The salient feature of this graph is the fact that clearance was not achieved. Therefore phagocytosis by hemocytes was inadequate.

The second line of evidence in support of my hypothesis about the clearance mechanisms derives from an experiment using colloidal carbon injection. This is very similar to work unknown to me at the time, reported by Stuart in 1968. Because of the superficial position of the vena cava cephalica of this octopus, it was possible to visually follow clearance of the carbon from the blood. The rate of clearance - subjectively measured - coincided with clearance data for bacteria. Most significantly, however, the site of clearance in the octopus is very clearly defined. This was determined in the following way. An experiment was conducted in which an octopus was sacrificed and thoroughly dissected 24 hours after receiving an injection of colloidal carbon. Signs of darkening were looked for in the kidneys, stomach, caecum, liver, blood vessels, brain, buccal mass, ovary, oviduct, esophagus, rectum, intestine, nerves and gills. Only the gills showed evidence of carbon accumulation. The white body and salivary glands, reported by Stuart (1968) to be clearance sites, were not checked. Further research is now required to establish whether particle-laden phagocytes leave the circulation in these specialized tissues, or whether the particles are not phagocytosed by amoebocytes in the blood but are agglutinated and phagocytosed by special cells in the gills and possibly elsewhere.

Gills in aquatic invertebrates have been implicated in much more than respiration, as their name implies. Feeding, excretion and osmotic balance are functions they perform in certain species. To this list we may now add blood clearance.

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SAMOANA OF THE SOCIETY ISLANDS (PULMONATA: PARTULIDAE)

Yoshio Kondo

ABSTRACT

The new species *Samoana burchi* from Tahiti is described and compared conchologically and anatomically with its close relatives, *S. attenuata* (Tahiti, Moorea, Tahaa, Raiatea, Borabora), *S. annectens* (Huahine) and *S. diaphana* (Moorea). *Samoana solitaria* (Crampton) is synonymized with *S. attenuata*. *Samoana burchi* is hypothecated to be ancestral to *S. attenuata*, which spread to all islands and gave rise to *S. diaphana* and *S. annectens*.

The land snail family Partulidae includes 3 genera and about 126 species: *Eua* with 4 species, *Samoana* with 22 and *Partula* with about 100 species (Kondo, 1968).

Four species of *Samoana* are credited to the Society Islands: *S. attenuata* (Pease) of Tahiti, Raiatea, Tahaa and Borabora; *S. annectens* (Pease) of Huahine; *S. diaphana* (Crampton & Cooke) and *S. solitaria* (Crampton) from Moorea. They co-exist with 66 forms of *Partula*.

Samoana solitaria is here reduced to *S. attenuata;* a new species, *S. burchi*, is here added to Tahiti.

Table 1 presents a bird's-eye view of the distribution of 4 *Samoana* species in the main Society Islands. *Samoana attenuata* inhabits 5 islands: Tahiti, Moorea, Raiatea, Tahaa and Borabora; and it may possibly be uncovered on Huahine when its highlands are searched. *Samoana annectens* and *S. diaphana* are considered to be derivatives of *S. attenuata*. A second species of *Samoana*, derived from *S. attenuata*, may be expected on Raiatea-Tahaa, to judge from the examples of Huahine and Moorea. Owing to the tiny remnant of native forest on Borabora, no derivative of *S. attenuata* may be anticipated here. *Samoana burchi* is hypothecated to be parental to *S. attenuata*, which in turn gave rise to *S. annectens* and *S. diaphana*.

Samoana annectens and *S. diaphana* have very thin shells; *S. annectens* is a medium altitude (ca. 500 ft.) species which exudes copious sticky slime; it is said to be excessively rare by Garrett (1884, p 66). (Montague Cooke and the author (Kondo) collected 65 adults at 1 station (only) in 1934); *S. diaphana* is a rare highland (ca. 2000 ft.) species.

Samoana attenuata has a heavy shell (except for those populations on Moorea), it inhabits medium to high altitudes (ca. 300-1900 ft.) and is scarce. *Samoana burchi* has a heavier shell, inhabits high altitudes (3200-4700 ft.) and is rare.

Between 1965 and 1971, the U.S. National Science Foundation enabled the Bernice P. Bishop Museum's Division of Malacology to conduct field researches on archaic land Mollusca Achatinellidae and Partulidae under grants GB-3974 and GB-6450 in the Melanesian region (Solomon Islands, Bismarck Archipelago, New Guinea, the D'Entrecasteaux Islands, the Louisiade Archipelago, New Hebrides, the Loyalty Islands and Lau of the Fiji Islands) and the Polynesian region (Tonga, Samoa, the Society Islands, the Marquesas Islands and Juan Fernandez). The anatomical monograph on Partulidae, which must emanate from the living animals

TABLE 1. Distribution of *Samoana* in the Society Islands

Species	Island					
	Borabora	Tahaa	Raiatea	Huahine	Moorea	Tahiti
S. attenuata	X	X	X		X	X
S. annectens				X		
S. diaphana					X	
S. burchi						X

collected in those places and preserved in the Bishop Museum collection, is still undergoing preparation: dissection, description and illustration.

In the Polynesian region in 1970, Bishop Museum Research Associate John Peake of the British Museum (Natural History) complemented the author's field work in Marquesas. Bishop Museum Research Associate J. B. Burch of The University of Michigan's Museum of Zoology and his assistants (James N. Cather, John B. Burch, Jr., Evin Oshima and C. M. Patterson) carried out field work on the subspecies of *Partula otaheitana* (Bruguiere) of Tahiti; searched for *Samoana solitaria* (unsuccessful) and *S. diaphana* (successful) on Moorea; and made general collections on Raiatea and Borabora. Harry S. Ladd of the U.S. Geological Survey was consultant throughout, but only the author (Kondo) must be held responsible for hypothetical statements on larger Pacific land masses and their subsidence.

For the privilege of working in the Society Islands and Marquesas, we are grateful to the Government of French Oceania and in particular to Dr. Henri Lavondes, Director of ORSTOM (Office De La Recherche Scientifique Et Technique Outre Mer) of Papeete, Tahiti.

This paper, which describes the shell, genital anatomy and pallial complex of a new species of *Samoana*, is dedicated with great pleasure to J. B. Burch, who, with his assistants, discovered this species in the highlands of Tahiti Iti at 3200 feet on the plant *Metrosideros*. This new partulid species is then compared with *S. attenuata*, and this comparison is enlarged to include a discussion of all the species of *Samoana* of the Society Islands and a hypothesis of relationships proposed. *Samoana solitaria* is synonymized with *S. attenuata*, and in this connection the Philadelphia Academy of Sciences is thanked for the lengthy loan of the holotype and only specimen of Crampton's *S. solitaria* (ANSP 290231). In connection with *S. solitaria*, the team of J. James Murray, Jr. of the University of Virginia and Bryan C. Clarke of the University of Nottingham are gratefully thanked for 4 specimens of *S. solitaria* accompanied by their soft parts which provided proof of its generic standing.

Samoana burchi, new species (Figs. 1; 2-1 top left; 3A, B, C, D)

The shell (Fig. 1) is dextral, ovate-conic, thick, perforate and dark brown (burnt sienna of Ridgway's color standards). There are 5 1/3 whorls, the apex is obtuse, the upper whorls blending smoothly with the ultimate whorl to form an ovately conic shell, the last whorl being only slightly capacious; the whorls are only slightly convex, the sutures slightly impressed; the last whorl has a 1/2 mm wide single dark brown band at the peripheral line, the band commencing where the upper end of the outer lip meets the last whorl and swinging around the last

FIG. 1. *Samoana burchi,* holotype of new species from Tahiti. Scale = mm.

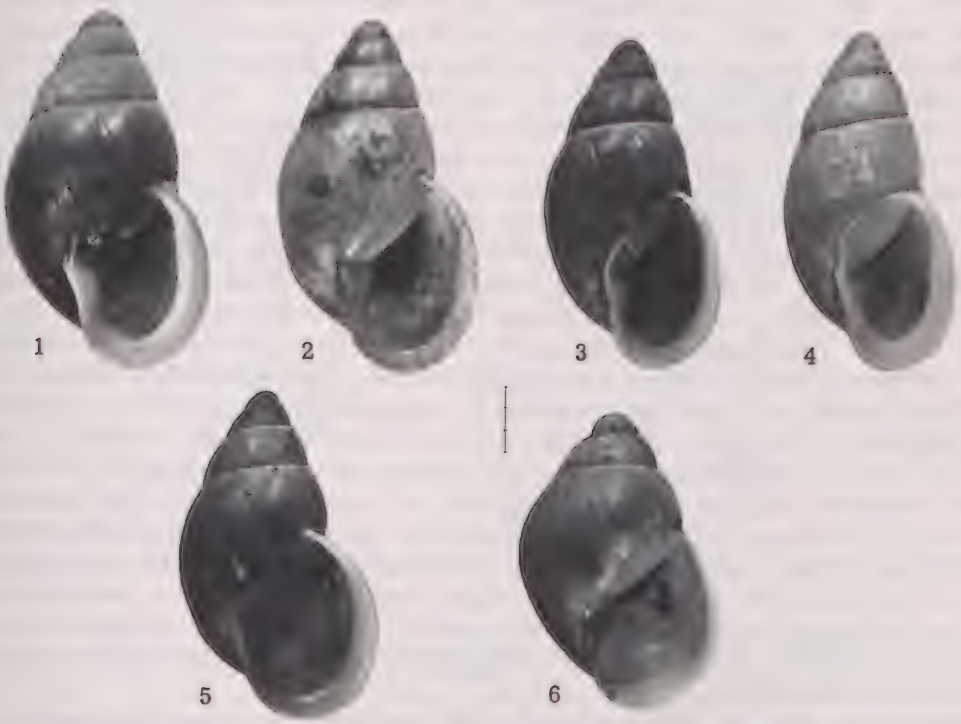

FIG. 2. Upper row: 1, *Samoana burchi,* holotype; 2, *Partula solitaria,* Holotype (now *Samoana attenuata*), Moorea; 3, *S. attenuata,* Moorea; 4, *S. attenuata,* typical, Tahiti. Lower row: 5, *S. annectens,* Huahine; 6, *S. diaphana,* Moorea. Scale = mm.

whorl at the peripheral line to end at the midline of the reflexed outer lip. The aperture is auriform, the white porcellaneous peristome exceptionally thickened, the terminal edge reflexed outwardly in the usual partulid manner and, in addition, forming a thick internal overhanging ledge which shrinks the size of the aperture considerably; the lip is thick, white and heavy throughout, does not form an expectable heavy parietal callus but instead a thin transparent one. The color is uniform burnt sienna throughout in juveniles, which in adults is eroded on the first 4 upper whorls to reveal a substratum of flesh brown.

Genitalia (Figs. 3A, B, C). The hermaphrodite gland (HG) (ovotestis) is small, bilobate or trilobate, the distal lobe being the smaller of the 2, having 20-25 finger-like follicles; the proximal lobe appears to be 2, but could be considered as 1, these lobes sharing a single efferent duct leading to the main hermaphrodite duct and having 25-30 follicles. The hermaphrodite duct or spermoviduct (HD) is convoluted and well filled. The albumen gland (AG) is robust, well developed, its follicles minute and numerous. The prostate gland (Pr) is well developed, its follicles minute, digitate and numerous. The upper uterus (Ut) was empty and deflated; lower uterus having one large white mature oval egg (e) with a thick shell (the egg later cracks and dissolves to release mature embryos into the vagina, thence to the outside via the atrium). The spermatheca (Sp) is 1/4 the length of the oviduct (the oviduct begins at the albumen gland and ends with the vagina), its tip is ovate, its stalk (SS) medium long, narrow and joins the oviduct at a low level. The vas deferens (VD) is free from the end of the prostate gland and runs down and alongside the uterus, turns up at the atrium and runs along the inner side of the penis to enter the epiphallus (Epi) near its apex. The penis (P) is short, stout, banana-shaped, and has a short inner curvature and a longer outer curvature. The penis plus epiphallus is 1/2 the oviducal length, the penis itself 1/4 the oviducal length; the epiphallus is thin and transparent. The penis has a thin sheath (Sh) housing a single curved tongue-shaped pilaster (Pil); this pilaster is attached along its entire length by its thin side to the sheath, the thick fleshy side being free and forming a shallow scoop or spoon on its inner side. The retractor muscle of the penis (RP) is very long, the distal end anchored to the diaphragm or floor of the lung (d); the proximal end of the retractor is inserted at the tip of the epiphallus but gives off a minute vestigial branch (rp), which hugs the vas deferens closely and inserts at the tip of the penis proper. Pilsbry & Cooke (1934, p 16) describe this peculiar retractor thus: "A club-shaped epiphallus (fig. 9, g) surmounts the penis, the penial retractor inserted at its apex, with a slender continuation to the apex of the penis." This slender continuation of the retractor is here called a vestigial branch. The epiphallus (Epi) is transparent and its internal structure consists of ridges of flesh appearing as tubercles; the epiphallus when split open (Fig. 3C, free hand drawing) reveals (a) a small group of 3 to 4 transparent transverse ridges above the entrance or orifice of the vas deferens into the epiphallus (VDO); (b) a group of 3 to 4 vertical ridges, the tops of which are crinkled into tubercles which begin at the entrance of the vas deferens (VDO) and build up fairly stout ridges ventrad to the midpoint, from which point these tubercles become weak and scattered below, near and at the entrance of the epiphallus into the penis proper. These 3 to 4 vertical ridges are interspersed by scattered tubercles. Transverse and vertical ridges are identical morphological structures.

The reverse side of the penis (Fig. 3B) is shown here in order to clarify its morphology and to illustrate how the vestigial penial retractor (rp) takes off from the main retractor (RP) as a slender thread from the tip of the epiphallus, running ventrad and parallel to the vas deferens (VD) to insert at the head of the penis (P); this also shows how the vas deferens adheres to the penis on the re-

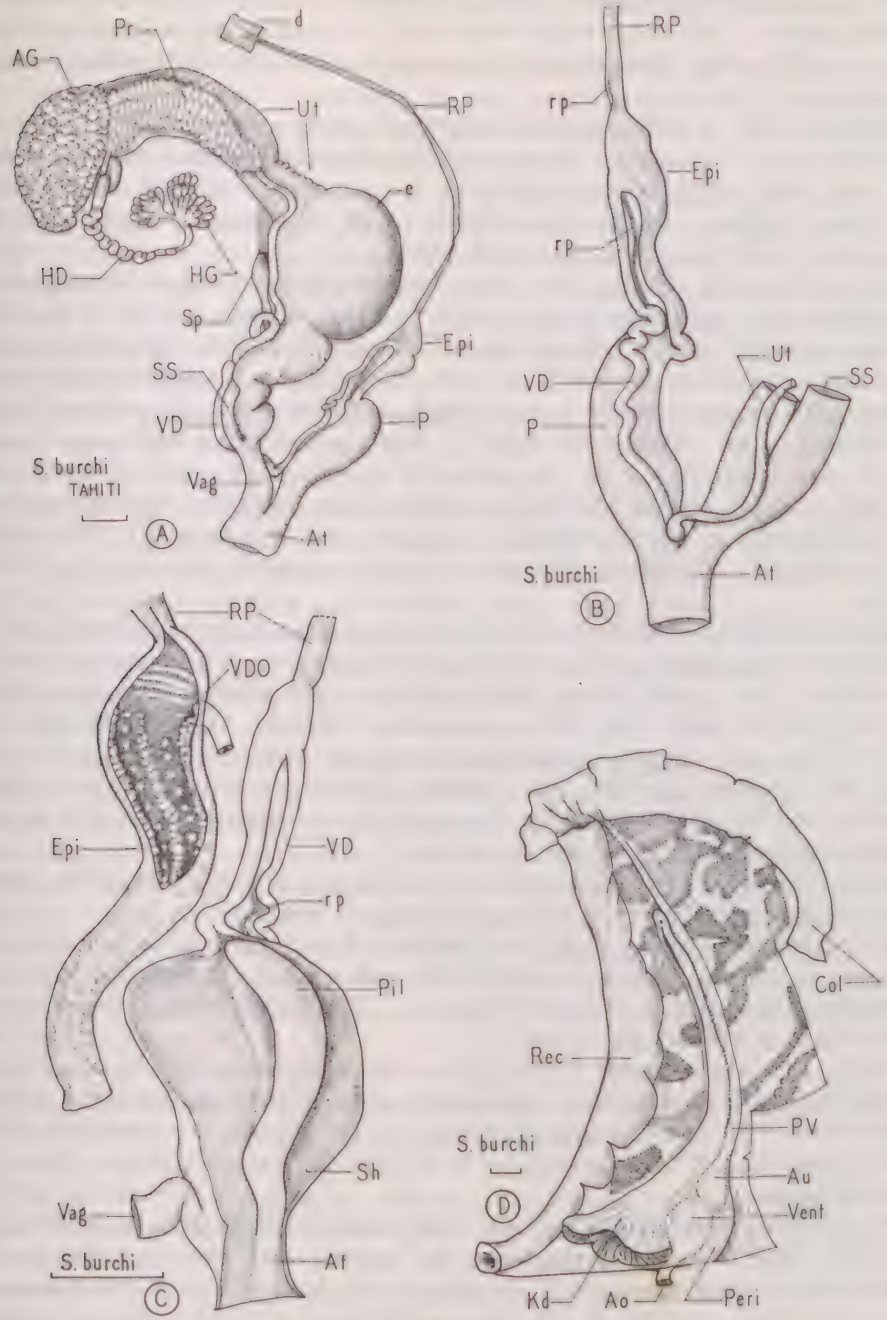

FIG. 3. A. *Samoana burchi*, genitalia. AG, albumen gland; At, atrium; d, diaphragm; e, egg; Epi, epiphallus; HD, hermaphrodite duct or duct of ovotestis; HG, hermpahrodite gland or ovotestis; P, penis; Pr, prostate gland; RP, retractor of penis; Sp, spermatheca; SS, spermathecal stalk; Ut, uterus; Vag, vagina; VD, vas deferens. Scale is 1 mm. Drawings by Y. Kondo. Outlined by camera lucida; completed free hand. B. *Samoana burchi*, enlarged reverse view of penis showing origin of vestigial penial retractor (rp) at insertion of main retractor (RP) on epiphallus and its continuation to penis proper. C. *Samoana burchi*, interior of penis and epiphallus. Pil, pilaster; Sh, sheath; VDO, orifice of vas deferens in epiphallus. Enlarged epiphallus drawn free hand. D. *Samoana burchi*, lung and pallial organs, and characteristic dark maculations of *Samoana*. Ao, aorta; Au, auricle; Col, collar; Kd, kidney; Peri, pericardium; PV, pulmonary vein; Rec, rectum; Vent, ventricle. Scale = mm.

verse side, being held loosely to the penis and oviduct by fine filaments.

All *Samoana* species are essentially the same in external and internal structure of their penes. The larger species, e.g., *S. cramptoni* of Eua Island, Tonga, have a more elaborate tubercle development in the epiphallus and a secondary smaller pilaster in the penis.

The lung (Fig. 3D) is conspicuously maculate with a silvery background; the jet black maculations are irregular in shape, being fingers of black regions coalescing here and there with adjacent maculations and contrastingly set off by the opaque silvery regions. This spotted characteristic of the mantle is characteristic of *Samoana* species when they are collected alive.

The kidney (Fig. 3D, Kd) is the usual orthurethran elongate triangular organ situated between the pulmonary vein (PV) and the rectum (Rec). It is prolonged and tapering anteriad until it terminates 1/4 way from the collar (Col), at which point it makes a recurvature posteriad and debouches via a small aperture at the apex. From this recurvature, a barely visible transparent filament of flesh continues posteriad, just visible to the 1/2 way point, then continues as a vague indication to its termination at the kidney's basal flare. H. B. Baker once remarked (pers. comm., 1954) that the partulid kidney's recurved filament of flesh seems to anticipate a sigmurethrous kind of ureter. In a second specimen of *Samoana burchi*, this recurving filament is not as clearly visible after the initial recurvature.

The pulmonary vein (PV) is clearly visible in *Samoana burchi*, and this may be due to the freshness of the specimen and the 2%+ 65% mixture of formalin-alcohol used as preservative. In most older specimens in the Bishop Museum, which are preserved in alcohol only, this vein is barely visible. The vein begins vaguely at the collar (Col), goes directly posteriad along the kidney and enters the auricle (Au) at the pericardium (Peri). Circulation continues from auricle to ventricle (Vent), thence into the body cavity via the aorta (Ao), which pierces the membrane at the posterior boundary of the pericardium.

The rectum (Rec) is a voluminous tube terminating at the anus at the right side of the collar at the same location as the pulmonary orifice.

Holotype of *Samoana burchi* (cat. no. 9006): 16 x 9 mm, whorls 5 1/3. Range of 6 paratypes (cat. nos. 206910 and 206915): 16 x 9 mm (3 specimens) to 17 x 9 mm (3 specimens); whorls 5 1/4, 5 1/3, 5 1/2. Additional 5 adult paratypes preserved entire in lots 206910 and 206915.

Type locality: Society Islands, Tahiti Iti or Tairapu Peninsula, Haoma highlands at head of Haoma Valley (altitude about 985 m (3200 ft.)), exclusively on *Metrosideros* plants 4 to 7 ft. above ground, usually on its leaves, occasionally on bark. July 7 and August 21, 1970; collected by J. B. Burch, James Cather, John Burch, Jr. and Evin Oshima.

Two counterparts of *Samoana burchi* were collected 36 and 39 years earlier than 1970, but their precise status was not known until Burch's abundant live-collected specimens confirmed their standing as *S. burchi*. Both specimens were collected on the trail leading to Mt. Aorai (altitude 2066 m = 6766 ft.) from the north: 1 specimen (cat. no. 106408) recently dead at 4100 ft. elevation by botanist M. L. Grant, June 4, 1931, labeled by Cooke *"Partula attenuata?"*; 1 specimen (cat. no. 136986) (18 x 9 mm) collected live at 4600-4700 ft., on fern, shrub or moss, by Donald Anderson and Yoshio Kondo, September 14, 1934, labeled by Cooke *"Partula* new species?". The direct line distance between Burch's locality and Aorai is 35 km (22 mi.). [After submittal of this manuscript, 2 live collected adult specimens colored dark brown were discovered among undistributed speci-

mens: Tahiti, Aorai Trail (presumably above 4100 ft.), February 1962, collected by Noel L. H. Krauss. These 2 specimens were too small a sample to have been recognized as a new species.]

The apical half of Grant's specimen of *Samoana burchi* had been eaten by some animal, leaving intact the residual ultimate whorl, plus 3/4 penultimate whorl; its color was light brown with a conspicuous linear 1/2 mm wide peripheral band of darker brown encircling the ultimate whorl.

The Anderson-Kondo specimen is 18 x 9 mm, whorls 5 1/2, almost entirely eroded to its chalky substratum, with fragmentary traces of epidermis remaining, among which traces of the peripheral band are discernible.

This peripheral band is clear in *Samoana cramptoni* (Pilsbry & Cooke) of Eua Island, Tonga as its figure shows (Pilsbry & Cooke, 1934, fig. 4). This linear band is a characteristic of nearly all species of *Samoana*, and is faint to barely visible in most species.

All known species of Society Islands *Samoana* were dissected for certification of generic standing and for comparison with *S. burchi*. These are *S. attenuata* (Pease), *S. annectens* (Pease) and *S. diaphana* (Crampton & Cooke), and their genital anatomy is treated together in the sections to follow, subsequent to their conchology. In brief, their genital anatomy (Figs. 4A, B, C, D) is closely similar and, as a purely verbal description, is considered insufficient for this report. The figures are published here as visual proof of their close relationship.

Samoana attenuata (Pease, 1864) was first described in the *Proc. zool. Soc., London*, 1864, p 672, as *Partula attenuata*. Pilsbry cites it in the *Manual of Conchology* (sec. ser.), vol. 20: 198, pl. 24, figs. 1, 2, 3, 4, 1909, and gives its complete synonymy.

Samoana annectens (Pease, 1864) was described as *Bulimus annectens* in *Proc. zool. Soc., London*, p 671. Pilsbry (1909) cites it in *Manual of Conchology*, 20: 254, pl. 24, figs. 5, 6, and gives its full synonymy.

Samoana diaphana (Crampton & Cooke, 1953) was described as *Partula diaphana*, *Occ. Paps. Bernice P. Bishop Mus.*, 21(8): 148, fig. 3, f.

Crampton (1916, p 30) was able to collect only 2 or 3 specimens of *Samoana attenuata* and was therefore unable to treat this species in the same way he did the 6 other Tahitian species of Partulidae. He also collected *S. attenuata* on Raiatea and records the treetop habitat of this species, which was detailed by Garrett (1884, p 70).

Samoana burchi compared with *S. attenuata*, *S. annectens* and *S. diaphana* (Fig. 2; Table 2)

Hypothesis: All Society Islands species of *Samoana* are derived from a common ancestral stock relatively recently as measured by geological time. *Samoana burchi* represents this stock and can be considered the immediate ancestor of *S. attenuata*. From *S. attenuata* evolved *S. diaphana* on Moorea and *S. annectens* on Huahine.

When *Samoana burchi* and *S. attenuata* are compared side by side (Fig. 2-1, 2-4; Table 2), these 2 species contrast themselves immediately and unmistakably. The dark brown *S. burchi* stands out conspicuously against the light corneous *S. attenuata;* the broadly straight ovate-conic *S. burchi* contrasts itself against the slim streamlined torpedo-shaped *S. attenuata;* the obtuse tip of *S. burchi* is in contrast to the sharp tip of *S. attenuata;* the whorls of *S. burchi* are convex, the whorls of *S. attenuata* almost flat. The shell of both species is solidly constructed,

but thicker in *S. burchi*.

Samoana burchi is most closely related to *S. attenuata* (but *S. attenuata*'s nearest relative is *S. annectens*). *Samoana burchi* is confined to Tahiti; *S. attenuata* has an almost universal distribution in the Society Islands (see Table 1), namely, Tahiti, Moorea, Tahaa, Raiatea and Borabora (but not Huahine). *Samoana attenuata*'s Huahine counterpart may be the closely related *S. annectens;* but there is a possibility that the aboriginal *S. attenuata* which gave rise to *S. annectens* may yet be found on Huahine.

On all islands (except Moorea), *Samoana attenuata* has stabilized to a definite form which is extremely streamlined and is characterized by a narrow elongate torpedo shape. Garrett (1884, p 71) says, "Its most essential characters are its graceful oblong-conic shape, narrow body-whorl, uniform whitish horn color and broadly expanded white lip." This torpedo shape is due to a peculiar compression of the ultimate whorl's left side, which reduces the diameter of this whorl, making it narrow instead of expansive, thus giving the entire shell a slim streamlined appearance.

Samoana attenuata and *S. annectens* are very closely related, and *S. annectens* (Fig. 2-5) appears superficially to be a mere variant of *S. attenuata* (2-4). However, the following concrete differences disallow the unification of *S. annectens* with *S. attenuata:* the living animal of *S. annectens* exudes copious slime when collected and is extremely sticky, whereas the animal of *S. attenuata* produces little slime, which means that there is a physiological difference between the two. [Cooke wrote in his field note book on *S. annectens* 136060 station 971 of September 30th 1934: "...the animals of this species are especially sticky unlike any *Partula* I have handled."] The shell of *S. annectens* is thin, fragile, pellucid, oblong-ovate (not torpedo-shaped), shorter, has less whorls, and the aperture is wide open, the lip thin. In contrast, the shell of *S. attenuata* is thick, solid, opaque, torpedo-shaped (not oblong-ovate), longer, has more whorls, aperture is narrow, the lip thick. But *S. annectens* does show a slight perceptible compression on the last whorl, which definitely relates it to *S. attenuata*.

Because *Samoana attenuata* and *S. annectens* are closely related, a direct comparison between *S. burchi* and *S. annectens* verbally is redundant. Differences between *S. burchi* and *S. annectens* may be adduced by comparing their figures (Fig. 2-1 versus Fig. 2-5) and studying Table 2.

The contrast between *Samoana burchi* and *S. diaphana* is easily visible from their photographs (Fig. 2-1 versus Fig. 2-6), which illustrate a brown, solid, ovate-conic *S. burchi* against a corneous, thin, fragile, semi-globose *S. diaphana*. *Samoana burchi* is much longer and has more whorls than *S. diaphana;* its lip is thick and heavy, while it is thin and barely formed in *S. diaphana*. Only in *S. burchi*'s blunt tip and *S. diaphana*'s obtuse tip are these species in any way close.

Samoana solitaria reduced to *S. attenuata*
(Figs. 2-2, 2-3, 2-4; Table 3)

Kondo (1968, p 75) transferred *Partula solitaria* to the genus *Samoana* on the evidence of Crampton's description of the *solitaria* egg being disproportionately large and comparable only to that of *S. fragilis* of Guam, the egg shell heavily charged with calcareous substance (1932, p 28, 29). The status of *solitaria* in *Samoana* was verified by the genitalia of the Clarke-Murray specimens.

It is regretful to have to reduce *"Partula" solitaria* Crampton to *Samoana attenuata* (Pease), but this has to be done. Crampton's and Clarke-Murray's specimens are too close to *attenuata* to be separated into a separate species.

TABLE 2. Shell characteristics of Society Islands *Samoana* species.

Character	Species			
	S. burchi (Fig. 2-1)	*S. attenuata* (Fig. 2-4)	*S. annectens* (Fig. 2-5)	*S. diaphana* (Fig. 2-6)
Color	brown	corneous	corneous	corneous
Length (mm)*	16-18	14-18	14-15	14-16
No. whorls**	5 1/3	5 1/3	5	4 3/4
Structure	solid	solid	thin	thin
Shape	ovate-conic	torpedo	oblong-ovate	semi-globose
Apex	blunt	sharp	sharp	obtuse
Lip	thick	thick	thin	thin
Last whorl	not compressed	compressed	compressed	not compressed

*Range of samples
**Average of range

TABLE 3. Comparison of shell characters of *Samoana attenuata* and *S. solitaria*.

Character	Typical *S. attenuata* (Fig. 2-4)	Crampton's *solitaria* (Fig. 2-2)	Clarke-Murray's *solitaria* (Fig. 2-3)
Color	corneous	corneous	light brown
Size (mm)	16 x 8	16 x 9	15 x 8
No. whorls	5 1/3	5 1/2	5 1/3
Structure	thick	thin	thin
Shape	torpedo	ovate-conic	streamlined
Apex	sharp	sharp	sharp
Lip	thick	thin	thin
Last whorl	compressed	compressed	compressed

If a separation were to be insisted upon, the Clarke-Murray specimens must by necessity be given a separate name from *solitaria* for this reason: they differ as much from *solitaria* as *solitaria* does from typical *attenuata*. Creation of artificial species would be a disservice to partulid taxonomy.

Crampton's holotype and only specimen of *Partula solitaria* (ANSP 290231), Clarke-Murray's 4 specimens of *solitaria* (BBM 206920-922) and *Samoana attenuata* from Tahiti (BBM 136031 St. John, figured), Raiatea, Tahaa and Bora-bora were compared simultaneously under a low power microscope and the differences are catalogued in Table 3. The comparative analytical columns provide ample proof that *S. attenuata* and the 2 kinds of *solitaria* are similar in all

respects except in 3 non-critical differences. Their photographs (Figs. 2-2, 2-3 and 2-4) provide good support of their similarity. Stripped of all similarities in Table 3, the following non-critical differences emerge: St. John's Tahiti *attenuata* (Fig. 2-4) is corneous, torpedo-shaped, heavy; Crampton's Moorea *solitaria* (2-2) is corneous, ovate-conic, thin; Clarke-Murray's Moorea *solitaria* (2-3) is light brown, streamlined but not typically torpedo-shaped, thin. These differences provide the principal contrasts among these 3 forms, but these differences are not significant enough to separate each one as a separate species. They are all *S. attenuata.*

Both the Crampton specimen and the Clarke-Murray sample must be considered deviants from the typical. Large samples from several Moorea localities should provide typical *S. attenuata.* It is curious that these samples of *S. solitaria,* collected in the vicinity of each other in inner Faatoai Valley, should differ so much from each other, the most conspicuous difference being the corneous color of Crampton's holotype and the light brown color of the Clarke-Murray samples.

Scarcity of *Samoana*

Scarcity is the commonest characteristic of all *Samoana* species of the Society Islands. The following adult specimens are in the Bishop Museum: *S. attenuata* 40, *S. annectens* 64, *S. diaphana* 3, and *S. burchi* 7.

Garrett's remarks on the rarity of *attenuata* (1884, p 70-71) is worth repeating and might apply to all *Samoana* of the Society Islands: "Owing to the peculiar habit of living on the foliage near the tops of trees, it easily escapes observation. It occurs more rarely at Tahiti, where it has, also, a wide range, and, like the Raiatea shells, is confined to the upper portions of the valleys." The treetop habit of *S. attenuata* was noted by Crampton (1916, p 30), the Mangarevan Expedition collectors and by Clarke (if his notes are interpreted correctly; see below under genitalia).

Genitalia of *Samoana attenuata, S. annectens* and *S. diaphana* compared with *S. burchi* (Figs. 3A-D, 4A-D)

All *Samoana* species of the Society Islands and elsewhere are characterized as follows: right ommatophore and its retractor passing through the penio-oviducal angle; penis innervated by cerebral ganglion.

The conspicuous feature of *Samoana* when collected alive is the spotted or maculate condition of the mantle and lung, which are readily seen through the semi-transparent shell.

The genitalia of *Samoana burchi, S. attenuata, S. annectens* and *S. diaphana* are similar, there being no special characteristic setting off any single species from the others, and this is construed as a testimony that the separation of these species from their parental stock is geologically recent.

The chief characteristic of the male genitalia is the short stout penis which is bent into a shallow curve like a turgid banana, the outer curvature having a greater length than the inner curvature. This is caused by an internal fleshy pilaster shaped like a club, formed like a scoop, and adhering to the penial sheath lengthwise. A well formed semi-transparent to transparent epiphallus attaches at the apex of the penis. The principal penial retractor muscle is long and robust, and is attached to the apex of the epiphallus, from which point a minute vestigial muscle is given off to attach to the apex of the penis proper. The vestigial nature of this minute penial retractor (rp) is evident; it surely cannot function as a

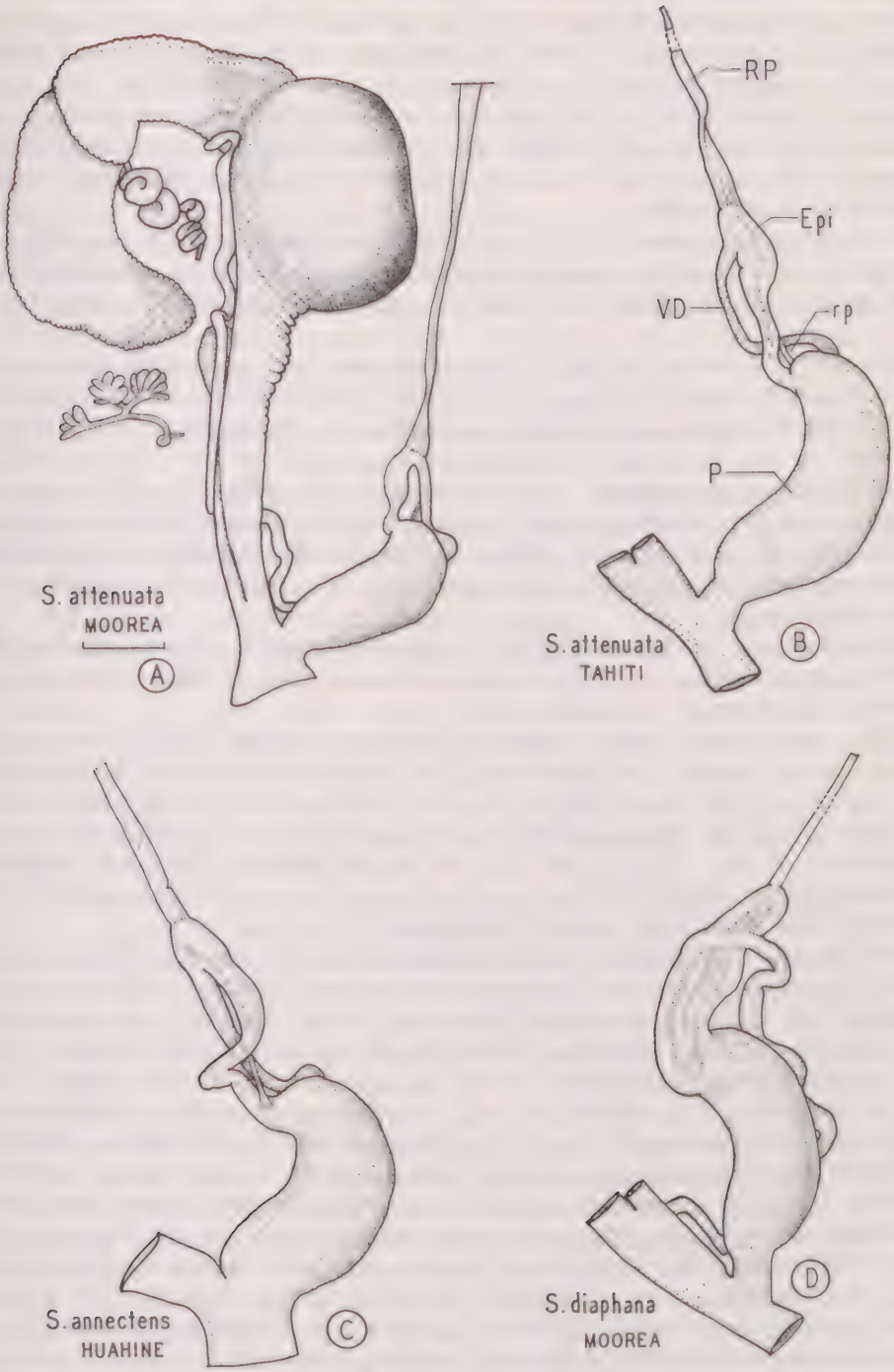

FIG. 4. A. *Samoana attenuata*, Moorea, genitalia, HG drawn free hand. B. *Samoana attenuata*, Tahiti, penis. C. *Samoana annectens*, Huahine, penis. D. *Samoana diaphana*, Moorea, penis. Scale = mm.

working retractor as does the large principal penial retractor (RP). The penis proper is 1/4 the oviducal length; the penis plus the epiphallus is 1/3 to 1/2 the oviducal length.

Crampton's *Partula solitaria* was suspected to be a *Samoana* in 1962 on the following evidence by Crampton (1932, p 28-29): "Egg capsule heavily charged with calcareous substance." And "In addition, the disproportionately large size of the egg is unique; only in *P. fragilis* of Guam is this equalled." Its transfer to *Samoana* by Kondo (1968, p 75) was confirmed by Clarke and Murray's gift of 4 specimens from Moorea, for which we are very grateful: the genital anatomy of their specimens proved that they are *Samoana*; the shells provided evidence that *S. solitaria* is *S. attenuata*.

Samoana attenuata (previously *solitaria*) of Moorea (Fig. 4A): Genitalia like that of *S. burchi*, *S. annectens* and *S. diaphana* in all respects. Ovotestis 3-lobate, albumen and prostate glands well developed; 1 mature egg at a high level in the uterus.

On Moorea, in Faatoai Valley, *S. attenuata* was collected near the same station that Crampton collected it (1932, pl. 13, F, p 26). Clarke's field notes are paraphrased here: Collected by Bryan and Ann Clarke on Moorea, inner basin of Faatoai Valley, altitude 360 m, on *Pandanus*, *Freycinetia*, *Angiopteris* and *Cyrtandra*, canopied by an unidentified leguminous tree, 18 September 1968. Snails were on shrubs and trees about 3 m above ground, usually higher than *Partula taeniata*. In the living animals, the dark brown pattern of the mantle pigment shows through the semi-transparent shell as spots as in *diaphana*. Snails died in captivity and were preserved in alcohol.

Samoana attenuata of Tahiti (Fig. 4B) was dissected to determine the existence of any differences from the Moorea *S. attenuata* and is figured in this paper as visual proof that there is no difference.

On Tahiti, in Papenoo Valley, *Samoana attenuata* (BBM 206917) was found at an altitude of about 1000 ft., on *Hibiscus*, collected by J. B. Burch, James Cather, John Burch, Jr. and Evin Oshima, 27 July 1970. Burch and company collected 4 adult specimens in Papenoo and 5 other adults from other parts of Tahiti, a good index of scarcity. Specimens of *S. attenuata* figured (Fig. 2-4) and tabulated (Table 2) as typical (BBM 136031, 1 only), from Papenoo Valley, altitude 1400 ft., were collected by Harold St. John, 16 October 1934.

Samoana attenuata of Tahaa (not figured here) was dissected in 1954; the drawing and description show close similarity to Moorea and Tahiti *S. attenuata*.

On Tahaa, Mt. Purauti, *Samoana attenuata* (BBM 136159) was collected at an altitude of 1200-1500 ft., high up on *Alyxia*, *Nauclea* and several other plants, by Clifford Gessler, Donald Anderson and Yoshio Kondo, 11 October 1934.

Samoana annectens of Huahine (Fig. 4C) was dissected in 1954 and again in 1972. The penis was the same as in *S. burchi*, *S. attenuata* and *S. diaphana* in all respects. The 1972 specimen was heavily pregnant with 5 elliptical heavily calcareous white eggs, which illustrated very well the stages of embryonation in *Samoana*. The upper 3 eggs were large, thick shelled, white; the first and uppermost with a tiny beginning crack; the second egg had a crack 3/4 around the egg shell; the third egg was without a crack. The 2 lowest and more mature eggs were in advanced egg shell dissolution: the 4th egg had a crack all around the shell with the dissolving regions showing as empty spaces, revealing glimpses of the developing embryo enclosed in albumen; the 5th and most mature egg was actually an emergent embryo with most of the egg shell dissolved, the remnants thin and fragile. The emerging embryo revealed the embryonic shell (protoconch), its apex pointing towards the vagina, its forebody pointing towards the upper uterus.

The ovotestis was 4-lobate; the albumen and prostate glands well developed.

Samoana attenuata of Huahine (Fare, BBM 136060) was collected at an altitude of 400-500 ft., on shrubs, by Charles Montague Cooke, Jr. and Yoshio Kondo, 30 September 1934.

The Partulidae is an ovoviviparous family. The description of eggs and resorption of their shelly capsule as described for *Samoana annectens* is the same for all species of *Samoana*. In the genera *Partula* and *Eua*, the egg shells are either thin or (rarely) there are eggs which have no shells at all. In instances where eggs have a calcareous covering, the lime is resorbed in the same way as in *Samoana* prior to release of the embryo. Ovulation and embryogeny of Partulidae will be fully covered in the anatomical revision.

Samoana diaphana of Moorea (Fig. 4D) has a penial complex the same as in *S. burchi*, *S. attenuata* and *S. annectens*. The inflated epiphallus in the figure is a temporary non-reliable characteristic. This specimen had 3 eggs in the uterus, the first 2 cracking, the last dissolving its egg shell. The ovotestis was 4-lobate; the albumen and prostate glands were well developed.

Hypothesis of descent and dispersal

A hypothesis of descent and dispersal of the 4 *Samoana* species of the Society Group must not be left unsaid. My hypothesis is as follows: (1) *Samoana burchi*, or its ancestor, arrived and colonized a large single Society island naving a virgin environment occupied by no other Partulidae genus (no *Eua* or *Partula*) and began expanding and occupying favorable habitats. (2) From *S. burchi* evolved *S. attenuata; S. attenuata* expanded and pressed *S. burchi* out of its favorable habitats, forcing *S. burchi* inland and upwards into the highest altitudes, and dispersed uniformly over the entire large Society island. (3) *Partula* arrived, expanded, and by its great numbers swamped out *Samoana*, forcing it into the higher altitudes and into small isolated colonies. (4) The large Society island subsided, leaving above water the mountain tops now bearing their present names and the fragmented populations of *S. attenuata*, from which were evolved *S. diaphana* on Moorea and *S. annectens* on Huahine.

In accordance with Willis' 1922 Age and Area hypothesis, *Samoana attenuata* and not *S. burchi* should be nominated the oldest species of Society *Samoana* owing to its near universal distribution in the Society Group, whereas *S. burchi* is narrowly confined to the high mountains of Tahiti. However, the higher altitude of *S. burchi* (3200-4700 ft.) against the lower altitude of *S. attenuata* (300-1900 ft.) negates Willis' hypothesis by another postulate, which is: The highest altitudes must be the last refuge of the earliest form (*S. burchi*), yielding ground to the highly competitive newcomer (*S. attenuata*).

The postulate of a prior solo occupancy of a large single Society island is dependent upon two other hypotheses: (1) *Samoana* is older than *Partula* (Kondo, 1968, p 73) and traveled eastward in advance of *Partula*; (2) animal life dispersed generally eastward from the west in the Inner Pacific, a hypothesis accepted by many zoogeographers (see Gressitt, 1954, p 207-216 for references).

Accepting the above 2 hypotheses, it is possible to hypothesize that the older genus *Samoana* dispersed eastward long before the younger genus *Partula*, and colonized Society, Raivavae, Rapa and Marquesas Islands; that *Partula* moved eastward behind *Samoana* and colonized Society, too, but never reach Raivavae, Rapa and Marquesas, which lie east of the Society Islands and are occupied solely by *Samoana*. Stoppage of *Partula*'s further eastward migration must be attributed to subsidence of the pathways.

To test the above hypothesis, the roles of *Samoana* and *Partula* were reversed but found not applicable to the factualities of the case: if *Partula* were older than *Samoana* and migrated eastward in advance of *Samoana*, the islands of Raivavae, Rapa and Marquesas should today be occupied solely by *Partula* instead of *Samoana*, which is not the case at all.

Samoana attenuata's wide dispersal in the Society Group requires the helpful hypothesis of a large single island 300 miles long (Mehetia to Manuae) over which *S. attenuata* spread uniformly without the hindrance of *Partula*'s presence. A sequential postulate calls for the subsidence of this large island, an idea not acceptable to many zoogeographers before 1953. Mode of migration or dispersal must be attributed "chiefly by their own powers of locomotion" (Pilsbry, 1916, p 431).

The postulate of a vigorous *Partula* swamping out a non-competitive *Samoana* is tenable. There are 66 forms of *Partula* versus 4 *Samoana* in the Society Group. *Partula* is ubiquitous and occurs in profuse populations. Conversely, *Samoana* exists in small isolated populations in tiny numbers.

The theory of larger islands and archipelagos which have subsided (see Pilsbry, 1900b; 1916) is supported by recent drilling results on Bikini and Eniwetok (Ladd *et al.*, 1948, 1953). Ernst Mayr (1953, p 8) says: "It now appears possible that such archipelagos as the Tuamotus, Marshall, Gilbert, Ellice and Phoenix Islands are the last remainders of once flourishing groups of high volcanic islands, such as the Hawaiian Islands are today." And "Whatever its causes are, the concept of the sinking of the Pacific is of great importance to the zoogeographer. It may help to reconcile the differences between the land bridge builders and the adherents of the permanency of oceans and continents."

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BRIEF COMMUNICATIONS

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ANALYSIS OF A SAMPLE OF *CORBICULA MANILENSIS* PHILIPPI FROM THE PEARL RIVER, CHINA.[1] —The Asian clam *Corbicula manilensis* Philippi was introduced into the U.S.A. in the early part of the 20th century, its first recorded appearance being in the Columbia River, Washington, in 1938 (Burch, 1944). Since that time the species has expanded its range in North America to encompass all of the major river basins (Sinclair, 1971a,b). *Corbicula*, as does the introduced bivalve *Dreissena polymorpha* in Europe (Morton, 1969b), causes problems of fouling, particularly in water supply systems. *Corbicula*, being essentially an infaunal species, causes problems in gravels which are for ultimate use in the production of concrete, but it also clogs pipes and condensers. In the Delta-Mendota Canal, California, U.S.A., Prokopovich (1970) has reported that *Corbicula* has formed vast beds. In some places the number of specimens amounted to between 125,000 and 163,000/cu.ft. This can be compared with the reports of 114,000 specimens/m^2 of *Dreissena* in the Szczecin Lagoon, Poland (Wiktor, 1963). Information on *Corbicula* and *Dreissena* is at present being collected and collated by the U.S. Environmental Protection Agency and published as an annotated bibliography (Sinclair, 1971b).

In the 1930's Miller & McClure (1931) published a detailed account of the flourishing clam industry based around Canton in the Pearl River, China. The clam is thought to be *Corbicula manilensis* Philippi. The Cantonese people eat the clam at all times of the year in a number of different ways, but it is particularly favoured at the time of Chinese New Year, which usually occurs sometime in February. A number of scientists consider that *Corbicula* was introduced into the United States from Kwangtung Province, China, (i.e., the Pearl River basin) during the time of an influx of Chinese refugees into the United States. Significantly many Chinese immigrants worked on the Columbia River in the latter part of the 19th century (Fox, 1971), and Hanna (1966) has been told by residents of Asiatic origin in the Sacramento-San Joaquin Delta that the clams were brought in from China. It would thus be of interest to gain some information regarding *Corbicula manilensis* from what may be regarded as its natural range, i.e., China.

Materials and Methods. During the time of Chinese New Year (February 16th and 17th) 1972, a visit to the fish market in Aberdeen, Hong Kong, revealed that live *Corbicula manilensis* were being offered for sale. The clam is not cultivated in Hong Kong and it was thus suspected that the animal was imported. The seller confirmed that the animals came from Canton, the city located on the Pearl River and the site of clam cultivation in the 1930's described by Miller & McClure (1931). Hong Kong is located at the mouth of the Pearl River and is approximately 100 miles from Canton. Most of China's trade with Hong Kong and the rest of the world is via Canton; trading vessels from China arrive in Hong Kong continually. Such a source would thus seem to be highly possible.

A sample of the clams was purchased and upon return to the laboratory each specimen was measured along its greatest width, height and length to the nearest mm and an estimate of their age made by inspection of the growth rings of the shell.

Results. The overall dimensions of the specimens of *Corbicula* from the Pearl River were comparatively regular, as can be seen from Fig. 1 and from the ratio of width:height:length, which is: 1:1.38 (±0.20):1.46 (± 0.28). The height of the shell appears to be more regular than the length, and accordingly, this dimension has been used in the construction of a size frequency histogram of the overall sample (Fig. 3,A). The total sample has been broken up into the component age groupings following analysis of the growth rings of the shell (Fig. 4) (Fig. 3, B-G). It can be seen that the major age grouping in the sample possesses 3 growth rings, while only a very small percentage possess 2 growth rings. It would thus appear that the collection methods utilised by the clam farmers exclude the smaller animals. There is a progressive decrease in the number of animals possessing 4, 5 and 6 growth rings. One animal with a shell height of 4 cm possessed either 7 or 8 growth rings. The number could not be ascertained with final certainty, since the growth rings in the species appear to become progressively more obscure with increasing size (Fig. 4).

The growth curve of the population of *Corbicula* from the Pearl River was tested using a Walford plot (Walford, 1946; Ricker, 1958). Fig. 2 (A) shows that the figures for the mean shell heights of the 3/4, 4/5 and 5/6 growth ring animals approach the 45° line as expected if growth fits the Bertalanffy formula, $H_t = H_\infty (1-e^{-K(t-t_o)})$ (Bertalanffy, 1938), where H = height of the shell, t = age, H_∞ = maximum theoretical height and K = a growth constant. The specimen with a shell height of 4 cm was plotted as a 7-growth-ring specimen against the 6-growth-ring specimens, and it was seen (Fig. 2, A; black dot) that such an estimate did not fit in with the pattern of growth established by the earlier age groupings. The 6-growth-ring specimens were then plotted against a hypothetical 7-growth-ring age grouping of shell height 3.7 cm. The hypothetical 7-growth-ring age group was also plotted against the 4.0 cm specimen as an 8-growth-ring specimen. The results of this configuration fit well with the earlier estimate of the growth pattern exhibited by this species and continues to approach the 45° line. It would thus appear that the specimen of shell height 4 cm possesses 8 growth rings.

From the plot of $\log_e(H_\infty - H_t)$ against H_t (Fig. 2, B) it was determined by trial that the best values of H_∞ and the slope K were 5.1 and 0.169 respectively. From this data the slope of the Walford plot (k) was calculated from $k = e^{-K}$ as 0.933 and this has been drawn in as a broken line in Fig. 2 (A).

The theoretical value of H_∞ of 5.1 can be used in the earlier estimate of the ratio of shell width:height:length to give a mean maximum theoretical length of 5.4 cm. However, taking into account the range of such estimates it would appear that the maximum theoretical length of *Corbicula manilensis* from the Pearl River is of the order of 6.4 cm.

Discussion. The sample of *Corbicula manilensis* from the Pearl River, China, contained a predominence

of specimens with 3 growth rings. One specimen was found to possess 8 growth rings. Very few shells with 2 growth rings were present in the population and there were very few specimens under 21 mm in length. Miller & McClure (1931), reporting upon the clam industry in the Pearl River around Canton, showed that specimens as small as 9-10 mm were collected. These authors advocated conservation of the stocks by increasing the mesh size of the collecting dredges to permit capture of specimens over 25 mm only, i.e., 3-year old animals. The virtual absence of clams with 2 growth rings and of specimens under 21 mm in length in this sample possibly indicates that such a protection of the stocks is being enforced in the Pearl River today.

Most researchers regard the growth rings apparent on the shell of *Corbicula* as representing annual growth rings, i.e., that one ring is produced/annum. Certainly Miller & McClure (1931) regarded this as being so for the Canton population. Such a hypothesis apparently finds at least the tacit acceptance of some workers in the United States. Although such an opinion may well be true, it should not be accepted until the growth rates of a whole population have been followed at regular intervals over the course of a year. Fuji (1957) has showed that *Corbicula japonica* lives for only 3 or 4 years. *Corbicula japonica*, however, achieves a shell height of only 22 mm. Stańczykowska (1963) described *Dreissena polymorpha* as possessing a maximum of 10 growth rings and further considered this to be equivalent to 10 years growth. The findings of Clarke (1952) and Wiktor (1963) conflicted with this view, and Morton (1969a) finally showed that *Dreissena* produces 2 growth rings/annum, thus halving Stańczykowska's estimate of the age. It is not inconceivable that such a situation also exists in *Corbicula manilensis*, and studies at present being undertaken in Hong Kong on a population of *Corbicula* which have recently colonised Plover Cove Reservoir may elucidate this point. The maximum theoretical length of *Corbicula manilensis* has been calculated, using a Walford plot, and has been shown to be approximately 6.4 cm. Such an estimate finds close agreement with the observations of Prokopovich (1970) on the population of *Corbicula* inhabiting the Delta-Mendota Canal in the U.S.A. where shells of 6.2 cm have been found. The mean maximum theoretical height of *Corbicula manilensis* has been shown to be approximately 5.1 cm. Perhaps significantly *Dreissena polymorpha* also possesses a maximum length of 5.1 cm. This similarity may be especially important, since what is commonly regarded as "length" in heteromyarian bivalves, e.g., *Dreissena*, is in fact the distance between the umbo and the opposite margin of the shell, which is in reality the height. Such a similarity may be coincidental or it may give practical support to the concept of a close phylogenetic affinity between these 2 bivalve assemblages as suggested by Morton (1970) and Taylor, Kennedy & Hall (1972). However, little is known of such measurements in other bivalves and hence comparative data is unavailable.

Miller & McClure (1931) considered that the time of breeding in *Corbicula manilensis* from the Pearl River was from November to July during the cool winter months. It is in fact only "cool" in southern China until April and such an estimate of the duration of the breeding season would seem to be excessive. In Ohio, U.S.A., the time of breeding of *Corbicula* is from July to November. Although the timing of breeding in these 2 populations thus conflicts, it may well be that the species breeds as a response to temperature (as in *Dreissena* (Morton, 1969a)) and not to a human calendar. Further information to elucidate this point is needed.

It would appear that the population of *Corbicula* from the Pearl River, China, is somewhat similar both in appearance and in terms of shell size with that of the populations of *Corbicula* inhabiting the waterways of the U.S.A. Much more comparative data on these populations is needed, however, before a source of infection can be defined for the United States populations. In the meantime, one cannot preclude the possibility that such a source was the Pearl River, China.

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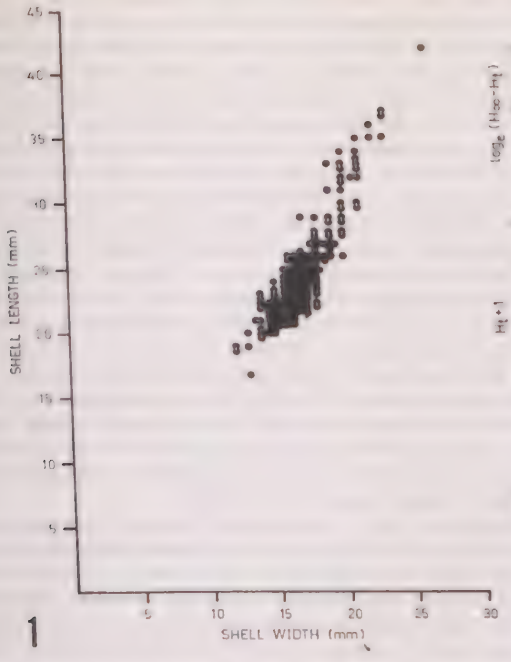

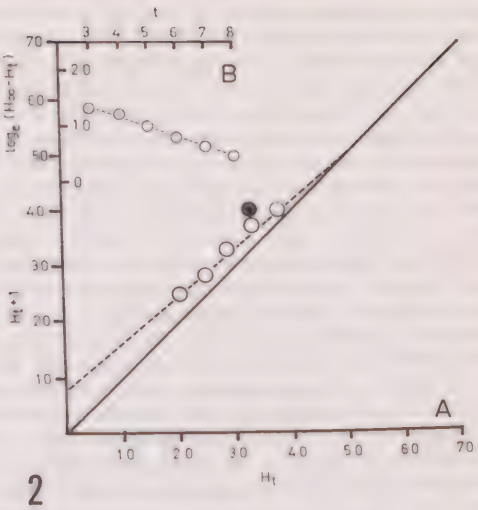

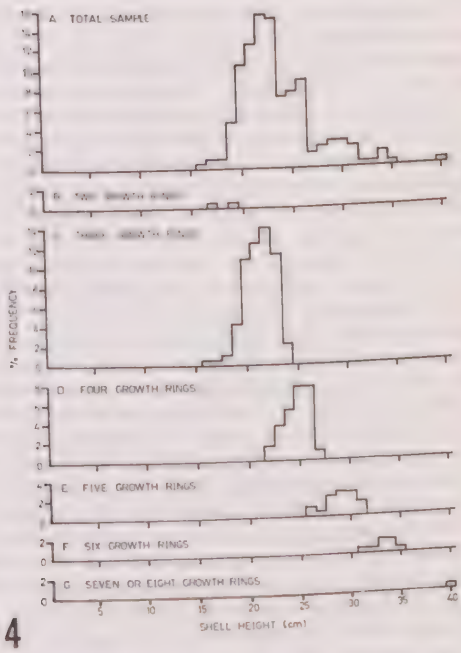

FIG. 1. *Corbicula manilensis*. The relationship between shell length and shell width.

FIG. 2. *Corbicula manilensis*. (A), A Walford plot for this species in which the mean height of each age grouping (H_t) has been plotted against the succeeding age grouping ($H_t + 1$); (B), Trial values of H_∞ have been used to give the best fitting line for a plot of $Log_e(H_\infty - H_t)$ against t. The slope K obtained from (B) has been used to calculate k. The Walford plot has been drawn in (A) with a dotted line using the calculated value of k and H_∞. (A) also shows (the black dot) the result of assuming the specimen of shell height 4.0 cm to possess 7, not 8, growth rings. It does not fit in with the pattern of growth established for specimens with fewer, more discernible, growth rings.

FIG. 3. *Corbicula manilensis*. Height-frequency histogram. (A), the total sample; (B-G), an analysis of the various age groupings as revealed by a study of the growth rings of the shell.

FIG. 4. *Corbicula manilensis*. The left shell valves of specimens from the sample from the Pearl River showing 2, 3, 4, 5, 6 and 7-8 growth rings. Such shells are referrable to the height-frequency histogram (Fig. 3).

* * * * *

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(1) I am grateful to Ralph Sinclair of the United States Environmental Protection Agency for reading this manuscript and for supplying me with information on the United States population of *Corbicula*.

HISTORICAL ASPECTS OF ALPHEUS HYATT'S WORK ON FOSSIL CEPHALOPODS.[1][2] — Alpheus Hyatt (1838-1902) was educated at Yale College and the Lawrence Scientific School of Harvard University where he graduated in 1862. During the American Civil War he served as a captain in the Union Army, but following his military service he returned to Harvard for advanced study under Louis Agassiz. Beginning in 1867, he was in charge of the fossil cephalopod collection at the Museum of Comparative Zoology at Harvard for the remainder of his life. The study of fossil cephalopods and their evolution became one of the major projects of his lifetime, and he became one of the foremost world authorities in the field. He served at various times as consultant in paleontology for the U. S. Geological Survey. He also did research on gastropods, bryozoans and sponges, and for many years was a leader in the field of science education.

In 1867 he became a curator for the Essex Institute at Salem, Massachusetts. When the Peabody Academy of Science was organized shortly thereafter and took over the scientific collections of the Essex Institute, Hyatt was one of the founding fathers, becoming a curator at the new Peabody Academy where he worked primarily with fossil mollusks, sponges and coelenterates. With his colleagues at Salem (F. W. Putnam, E. S. Morse and A. S. Packard, Jr.), he was a founder of the *American Naturalist* (1867) and the American Society of Naturalists (1883), for which he was the first president.

In 1870, Hyatt was appointed custodian for the Boston Society of Natural History, but 9 years later his title was changed to that of curator, a post he held for life. Also in 1870, he became part-time professor of zoology and paleontology at the Massachusetts Institute of Technology and 7 years later received a similar appointment at Boston University. That same year he organized his famous Teachers School of Science located in Boston. Between 1872-73, he visited Europe to study fossil cephalopods in various museums and the fossil gastropods at Steinheim in Germany (Hyatt, 1880).

Between 1880-86, Hyatt directed a sea-side laboratory near his summer home at Annisquam on Cape Ann, Massachusetts. This summer station led directly to the founding of the Marine Biological Laboratory at Woods Hole in 1888, when he transfered operations to that locality. In connection with his summer school at Annisquam, he had a schooner built for scientific exploration which he named the *Arethusa*. This vessel was used not only for field surveys and dredging studies at his summer school, but also for collecting trips to Anticosti Island, Newfoundland and Labrador in 1881 and 1885 for the collection of fossil cephalopods. Details of his summer laboratory and expeditions have been published by Dexter (1952, 1957) and Burbank & Dexter (1954).

Some typical excerpts from Hyatt's diary, with special reference to fossil cephalopods, recorded on his expedition to Anticosti and Newfoundland in 1885 follow: (10 July 1885) "We had found in the quarry the two extraordinary and perfect specimens of Piloceras and marked them with intense satisfaction for future work. — (11 July 1885) I had the pleasure of seeing the long and elegant forms of the *Orthoceras piscator* lying in the rocks. We dug out many specimens of these and of Gastropoda. — (12 July 1885) I went to the little islands in the harbor and on the outer one I found and collected several Nautili and marked the segment of a huge Beceptaulites. I also walked farther on to see about the Piloceratites and other fossils. — (15 July 1885) We walked across the isthmus to Old Port au Choise and from thence, by a broad path, probably a surveyor's road, to the cove and thence along the cliffs to our locality where we found the most remarkable display of cephalopods I have ever seen — we cut out two armed specimens which I thought were Armouchites, but could not possibly say. — (27 July 1885) The cherty limestone appears at Cape Norman under the light [light house] containing abundant Nautili and Orthoceratites more or less fossilized with chert and weathering often red. Above these in the last stratum we found similar fossils and the large Piloceras. — (31 July 1885) Got one exceedingly large and fine Piloceras and the number of siphons in the rocks was very remarkable. The specimens with remnants of the shell attached to the siphons were more frequent and we saw several besides those that were dug out. — (3 August 1885) Point Amon. Here we found the limestone coming down to the waters edge or nearly to it. We found at this point Archeocyathus in spots forming the entire mass of the rock. It seems to have grown in great masses closely associated and been buried up like corals, possibly in its own debris."

Altogether, Hyatt published about 50 papers and monographs on his studies of the fossil cephalopods. One of the first of importance was his catalog "The fossil cephalopods of the Museum of Comparative Zoology" (1865), published in the first Bulletin issued by the Museum of Comparative Zoology. It included 24 genera and 127 species described by Hyatt.

His first paper based upon his own field collections of fossil cephalopods was a study of Beatricea collected on an expedition to Anticosti Island in 1861 while still a student under Agassiz (see Dexter, 1954). Many specimens were collected at that time. Billings, who described the genus, thought it was a plant fossil, but Hyatt believed it to be a new order of mollusks allied to Orthoceratites. Today these fossils are regarded as hydrocoralline coelenterates.

Biographical sketches of Hyatt have been published by Morse, *et al.* (1902), Packard (1903), Crosby (1904), Brooks (1909) and Mayer (1911). The accounts by Crosby and Brooks include a fairly complete bibliography of Hyatt. His principal publications on fossil cephalopods in addition to his initial catalog (1865) already mentioned are as follows: "On the parallelism between different stages of life in the individual and those in the entire group of the molluscous Order Tetrabranchiata" (1867), "Genetic relations of Stephenoceras" (1876), "Genera of fossil cephalopods" (1883), "Genesis of the Arietidae" (1889), "Phylogeny of an acquired characteristic" (1894), "Bioplastology and the related branches of biologic research" (1895) and the posthumous monograph published with James P. Smith on "The Triassic cephalopod Genera of America" (1905).

Hyatt's major research centered around the evolution of the cephalopods. He was an advocate of orthogenesis and he developed in 1866 a law similar to the "biogenetic law" of Haeckel which Hyatt

called the "law of acceleration." E. D. Cope independently arrived at the same law at about the same time, but expanded it somewhat to include "retardation" (Cope, 1868; 1871). The principle then became known as the Hyatt-Cope Law of Acceleration and Retardation. Because Cope was better known through more frequent publication, some authors referred to the principle as the Cope-Hyatt Law, although Hyatt had slight priority of publication. This principle in brief meant that "Adult characteristics which are introduced in ancestral forms tend to re-appear at earlier and earlier stages" (Hyatt, 1880). Later (1889) he gave a more precise definition stating that "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then would be inherited in successive descendents at earlier and earlier stages, according to the law of acceleration, until they either become embryonic or are crowded out of the organization and replaced in the development by characteristics of later origin."

This principle became a cornerstone for the Neo-Lamarckian School of Thought developed in America by Hyatt and Cope, and was followed by such zoologists as Packard, Osborn and Jackson in the United States, by Herbert Spencer, Henslow, Turner and Gedden in England, and by Eimer and Nägeli in Germany. The Neo-Lamarckians emphasized the impact of the environment in the evolution of animal life.

While visiting the famous Steinheim sandpits in Germany, to study the fossil mollusks there, Hyatt wrote to his good friend Samuel Scudder in February of 1873. An excerpt from the letter which explains in greater detail Hyatt's views on the law of acceleration and retardation follows. "Speaking of Darwin and my views with regard to evolution it is really wonderful how much his book and his opinions have been misunderstood. When he spoke in one of his letters of the laws of growth and inheritance as paramount to Natural Selection in some cases I could hardly believe my eyes. He evidently considers that the law of Natural Selection is only one of the agencies by which animal organisms are modified and is quite willing to accept other laws especially those which depend upon growth. In fact, the man is not only wonderfully learned, but equally to be admired for his judicial fairness of mind and modesty. You will see by the paper on 'Reversions among Ammonites' that I have been making some advances towards what I consider a most desirable object, namely the reconciliation of Darwin's law of Natural Selection, etc. with our law of acceleration and retardation. Cope's law of retardation, for this is more properly his, is easiest to reconcile and Darwin himself suggests with reference to acceleration that characteristics, which are once introduced, may habitually become an integral part of the organization and inheritable at earlier periods by successive generations of individuals. These then are no longer modifiable by Natural Selection and the larger portion of the characteristics of the growth and development of an animal is removed from the category of those characteristics which may be subject to the action of external circumstances. The loose joint in our theory Darwin laid his finger on in his second letter to me. He shows that we do not account for the origin of the new adult characteristics by the law of acceleration. Thus starting with an animal which is 'a' in the adult, we find next one that is 'a' young and 'b' in the adult and then one that is 'ab' young and 'c' in the adult. Now acceleration expresses nicely the way in which 'a' and 'b' become younger or are earlier and earlier reproduced but how about their origin when first brought out in the adult ancestors? By what means do they come into being? The fallacy consists in the assumption that there is a progressive tendency in the organization itself which obliges it to become through growth something else of a given kind in the adult. Growth accounts for the increase in size, but is there really anything in the idea that the organization must develop new characteristics after the old ones have become youthful or embryotic? And supposing this to be so, are these newly developed characteristics in correlation with those that have preceded, have they the same reference to them, as an effect to its cause? Or, on the contrary, are they determined wholly by external circumstances, natural selection, etc.? I think I see a light on the horizon, but it is rather distant now. It seems to me that a careful study of the forms, that have passed through many geological epochs without much change, may do a great deal. There is only one *shell covered* form — the close, involute spiral which has survived all tests among the Cephalopods, though they start and end with every possible modification from the spiral to the straight. Now 'a priori' I am very much disposed to think that Natural Selection in its broadest sense determined which one of these forms should live, which one was best suited to withstand the geological revolutions which followed their introduction. In the same way it probably provided for the changes by which the straight shell became internal and succeeded in resisting all changes as an internal organ in the body of the Belemites and squid, etc., though wholly inadequate to resist many geological changes as an external straight shell. But everywhere in this selected form are certain elements in endless repetition, nature seems never tired of reproducing these elements of form with slight but ever diverging structural differences in the genetically connected series of species. Again these elements of form are repeated in each individual by growth in proportion to his place in his own series and even the degraded positions or declining races are not exempt but must go through a certain routine of retrograde metamorphoses. In these they undo what has been built up by time and growth, but it is done with due deference to these elements of form, and even the retrograde characteristics become inheritable. The former cannot I think be attributable to natural selection as I now understand it and the latter certainly not, as Darwin himself seems disposed to admit. There is here evidently a law of growth, not acceleration and retardation and not natural or sex selection, but something which includes both. The former, as Darwin suggests, is more a mode of development than a law of origin for characteristics and I begin to think that natural selection is about the same thing. That is the mode in which nature chooses from a certain series of definitively limited variations those which are best suited to the surrounding circumstances. If this is the case we must look for a law of growth of which these are the mere modes of expression. Having gone so far and being in a speculative spirit I will say

that I believe this law of growth will be the same for the individual as for the series and in a more comprehensive way for the whole animal kingdom and that it must also not only reconcile acceleration, natural selection, etc. together but must also be adjustable to the geological development of the earth. Cope is on this track, this much he has told me, and I hope he will find this law. He has qualifications which admirably fit him for the task, but it is a fearful one and much too great for me."

Neo-Lamarckian theories were largely dispelled by the work of Weismann, who first clearly pointed out the difference between germplasm and somaplasm. Near the end of Hyatt's life, Pavlov (1901) questioned the interpretation of Hyatt on the basis of stratigraphic sequence. Spath (1933), following Pavlov, reached conclusions diametrically opposed to those of Hyatt. J. Challinor, in Bell (1959), supported the conclusions of Spath. Both of these authors, however, overlooked the fact that Hyatt realized that many Ammonites uncoiled in the course of evolution (Hyatt, 1870), as well as advocating his interpretation of coiling-up with age, which belief has not been acceptable to recent authors.

In spite of modern changes of interpretation, Hyatt's basic descriptive work in classification and the stimulation he gave to the study of evolution among the cephalopods remain as significant contributions.

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Malacological Review, 1973, 6: 41-68

MOLLUSK SEMINAR
ANN ARBOR, MICHIGAN
25, 26 August 1972

(Proceedings of the *Society for Experimental and Descriptive Malacology*, 1972)

PROGRAM

Opening remarks, J. B. BURCH

Multi-disciplinary Contributions to the Study of Systematics and Evolution of Mollusks.

Convener, George M. DAVIS

Integrated approaches to molluscan systematics. George M. DAVIS.
Some current research on the genus *Bulinus*. J. B. BURCH.
The systematic position of *"Stagnicola (Bakerilymnaea) cubensis."* P. T. LoVERDE and J. B. BURCH.
Electrophoretic techniques in malacology: applications and pitfalls. E. H. MICHELSON.
Electrophoretic variations in foot muscle esterases in populations of some African *Biomphalaria* species. F. M. A. UKOLI.
The occurrence of hemagglutinins in some Basommatophora and Stylommatophora. Paul RUDOLPH.
Pigmentation variations in *Biomphalaria glabrata* and other Planorbidae. C. S. RICHARDS.
Breeding experiments with *Stagnicola elodes* and *S. emarginata*. Patricia A. AYERS and J. B. BURCH
The podocyst in pulmonate evolution. J. N. CATHER.
Comparative observations on speciation in two species of prosobranchs, *Gibbula cineraria* (Linné) (Trochidae) and *Littorina saxatilis* (Olivi) (Littorinidae). Jean M. GAILLARD.
Generic and specific taxonomic characters in succineid snails. C. M. PATTERSON.
Concluding remarks. George M. DAVIS.

General Session.

Convener, C. M. PATTERSON

Cytoplasmic localization in *Bithynia tentaculata* and its influence on development. N. H. VERDONK.
Ultrastructural development of *Ilyanassa*'s shell gland. Alex TOMPA.
Internal defense mechanisms of *Octopus dofleini*. C. J. BAYNE.
The role of galactogen in pulmonate snails. Esther M. GOUDSMIT.
Organic content of eggs and juveniles of an amphibious snail, *Pomacea urceus* (Müller), from the Venezuelan savannah and their ecological significance. Albert J. BURKY.
Activity patterns of the freshwater snail *Lymnaea stagnalis* (Say) exposed to sub-lethal elevated temperatures. Sharon C. McDONALD.
Reaction of pulmonate snails to temperature. Henry VAN DER SCHALIE and Elmer G. BERRY.
Nominal *Physa* species in Michigan with a brief review of systematics of the Physidae. George A. TE.
Apparent hybrids from a laboratory culture of *Lymnaea stagnalis* and *Bulimnea megasoma*. G. K. LINDSAY and J. B. BURCH.
Taxonomic problems in the Helisomatinae. G. L. PACE.
Bulinus sericinus from Ethiopia. S.-K. WU and J. B. BURCH.
Zoogeographical affinities between the naiad fauna of the Sydenham River, southwestern Ontario, and the Mississippi River basin. Carol B. STEIN.
On the distribution of Unionidae in the Sydenham River, southern Ontario. Arthur H. CLARKE.
Northern extensions of the Cumberlandian naiad fauna in tributaries of the Cumberland River in Kentucky. David H. STANSBERY.
Zoogeographical patterns in the marine bivalve fauna of the Canadian Arctic. Irene LUBINSKY.
A case for protecting the driftless area of the upper Midwest. Marc IMLAY.
Role of *Lymnaea stagnalis* (Say) and *Stagnicola reflexa* (Say) as intermediate hosts for *Plagiorchis noblei* Park, 1936. Harvey D. BLANKESPOOR.
Transmission of ostracods in snail aquaria. Y.-S. LIANG.
Incidence of a parasitic leech (*Marvinmeyeria* [=*Oculobdella*] *lucida* Moore) and two cercarial types in estivating *Stagnicola exilis* (Lea). Donald J. KLEMM.

ABSTRACTS OF PAPERS

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Multi-disciplinary Contributions to the Study of Systematics and Evolution of Mollusks

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INTEGRATED APPROACHES TO MOLLUSCAN SYSTEMATICS

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Abstract

An integrated approach to systematics involves selecting and using 2 or more methods in studying a population, with the intent for future comparisons with other populations. Techniques may be conchological, anatomical, cytological, biochemical, physiological, etc. A stereotyped approach is to be avoided (e.g., cytological data will not solve every problem in assessing relationships between organisms). Available techniques involve different levels of genetic manifestation. Comparative anatomy involves the end product of programming by tens of thousands of genes. Finding the deletion of 1 chromosome may indicate loss of hundreds or thousands of genes. Differences between taxa in an Rf value of a protein separated in a gel by electrophoresis may involve 1 gene.

Examples from the literature of integrated approaches are given below. (1) Species identification and inter-species relationships: Anatomical data showed that so-called *Tricula chiui* of Taiwan was actually *Oncomelania* and immunological studies showed closest genetic relationship to *O. h. formosana* of Taiwan (Davis, 1968, *Malacologia*, 7: 17-70). (2) Differentiation of sibling species: Chromosome number and karyotype analyses revealed the presence of sibling species in *Semisulcospira* of Lake Biwa, Japan. *S. habei yamaguchi* with the haploid chromosome number of 7 is readily confused with *S. decipiens* (n=12) and *S. multigranosa* (n=14) on the basis of adult shell morphology. Once separated by chromosome number, consistent characters in the embryo shells were found to differentiate the taxa (Burch, 1968, *J. Conchyliol.*, 107(1): 3-51; Davis, 1969, *Malacologia*, 7: 211-294). (3) Phylogenetic origin of the Pleuroceridae: Morrison (1954, *Proc. U.S. natn. Mus.*, 103(3325): 357-394) considered the Pleuroceridae to have evolved from marine Cerithiidae, and the Thiaridae from marine Modulidae. Immunological data (Davis & Suzuki, 1971, *Veliger*, 13(3): 207-225) showed a very close genetic relationship between Pleuroceridae, Thiaridae and the marine Potamididae, but not the Cerithiidae. Anatomical studies to date have not been of great value in predicting relationships made clear by immunological analyses. (4) Differentiating species groups: On the basis of anatomical data, Walter (1968, *Amer. malacol. Union, ann. Reps.*, 35: 23-25) concluded that recognition of traditional "genera" obscured more than it revealed in depicting relationships in the Lymnaeidae. Burch, *et al.* (1971, *Zool. Zh.*, 8: 1158-1168) through cytological and immunological data have shown that there are genetically separated species-groups, that shell morphology correlates with distinct species-groups and that certain anatomical features have undergone parallel evolution. Reliance on anatomical data alone in the Lymnaeidae actually obscures genetic relationships.

From the above examples the following points are derived: (1) The starting point for a systematic and evolutionary study is a population. It is essential that the initial population is unquestionably referred to an established type so that necessary historical-nomenclatural matters are firmly fastened. (2) No single technique can be used to differentiate species of all groups; e.g., anatomy is extremely useful in the Hydrobiidae, but causes confusion in the Lymnaeidae. (3) Detailed anatomical work coupled with the basic chromosome number does provide the widest and most meaningful platform for assessing relationships between taxa in the absence of prior work. As stated by Davis & Lindsay (1967, *Malacologia*, 5: 311-334): "Within a framework of precise anatomy and cytology, biophysical data have their useful place. Without this framework one is caught in a morass of disjunct molecular populations." (4) Biochemical techniques, with particular reference to immunology and electrophoresis, are extremely valuable tools to establish degrees of genetic homology, inferred rates of evolution within a species, and in establishing genetic markers. Immunological studies are best suited for analyzing macromolecular homologies where relationships to be assessed are those between closely related families, genera and/or species-groups. Depending on the rate of evolution and macromolecular divergence, it may or may not be possible to distinguish between congeneric species. Electrophoretic procedures are best used to analyze relationships between

congeneric species and between populations, especially in documenting the degree of infraspecific polymorphism. Considering the frequency of the presence of certain enzymes or other protein fractions to be under control of alleles, one can determine whether or not the alleles are in a steady state or are shifting in frequency. Greater polymorphism is interpreted as reflecting the greater ability of a species to respond to selective pressures, to adapt and to survive. Greater polymorphism reflects the potential for active speciation.

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SOME CURRENT RESEARCH ON THE GENUS *BULINUS*[1]

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Abstract

The African freshwater pulmonate snail genus *Bulinus* contains the intermediate hosts of human urinary schistosomiasis. Until recently, systematics of the genus seemed hopelessly confused in a complex of little-understood morphological variability. The beginnings of a more reasonable taxonomy were made by Mandahl-Barth (1957, *Bull. Wld. Hlth. Org.*, 17: 1-65). In a series of publications since 1960, we have shown that *Bulinus* is remarkable in that it contains a series of polyploid populations or species characterized by exact multiples of the basic chromosome number (x=18) of the family Planorbidae to which they belong. Some species have the normal diploid chromosome number (n=18, 2n=36), whereas various other species are either tetraploid (n=36, 2n=72), hexaploid (n=54, 2n=108) or octoploid (n=72, 2n=144). All polyploids, as well as some of their close diploid relatives, occur in the subgenus *Isidora* (= *Bulinus s.s.* in much past usage). This bulinine subgenus comprises the more northerly *B.* (*Isidora*) *truncatus* species group, whose members are mostly tetraploid (but with 1 octoploid species) and are readily capable of being infected with North African *Schistosoma haematobium*, and the more southerly *B.* (*Isidora*) *tropicus* species group, which is diploid (although it possibly contains a hexaploid species) and nearly always refractory to infection with *S. haematobium*. Chromosome numbers have provided a new light to the old problems of snail identification, taxonomy and recognizing potential intermediate host snails. Recent studies from our laboratory on various aspects of the biology and parasitology of *Bulinus* are Burch (1972, *Malacol. Rev.*, 5(1): 7-8), Burch & Lindsay (1970, *Malacol. Rev.*, 3(1): 1-18; 1971, *Zool. Afr.*, 6(1): 39-44), Lo (1972, *Malacologia*, 11(2): 225-280), Lo, Burch & Schutte (1970, *Malacol. Rev.*, 3(2): 121-126), Patterson (1971, *Malacol. Rev.*, 4(1): 27) and Wu (1971, PhD. Dissert., Univ. Mich., 149 p; 1972*a*, *Malacol. Rev.*, 5(1): 13-14; 1972*b*, *Ibid.*, 5(2): 95-164).

In the subgenus *Isidora* there are very few morphological differences between the various species, regardless of their chromosome number. The differences that do exist are slight. Karyotypic differences, other than chromosome numbers, also seem to be minor. However, each of the chromosome number groups can be distinguished readily by micro-Ouchterlony double diffusion precipitin tests, as well as by electrophoretic separations of foot muscle proteins. Therefore, chromosome numbers and biochemical differences still are the most reliable methods for separating the species or species groups, as observed previously (Burch, 1967, *Adv. Abstr. Contr. Fish. Aquat. Sci. India*, 1(4): 34-35; 1968, *Proc. Symp. Moll.*, Mar. biol. Assoc. India, Symp. ser. 3, (1): 10-15).

Cross-breeding experiments showed that diploid *Bulinus tropicus* from South Africa would produce fertile progeny when mated with diploid populations from as far away as Ethiopia, although in the latter case the cross was successful in one direction only, from Ethiopian to South African snails. Similar results were obtained when *B. tropicus* was crossed with South African *B. natalensis*. A few crosses between diploids and polyploids were successful, but hybrid offspring were sterile.

Infectivity experiments show that species belonging to the polyploid *Bulinus truncatus* group seem invariably to be susceptible to North African *Schistosoma haematobium*, and, with few exceptions, species of the diploid *B. tropicus* are refractory to infection. Therefore, areas containing *B. truncatus*-gp. species but without schistosomiasis haematobia should be carefully watched in regard to people immigrating from endemic areas.

Some recent studies along similar lines from other laboratories are Brown, Oberholzer & Van Eeden (1971*a*, *Malacologia*, 11(1): 141-170; 1971*b*, *Ibid.*, 11(1): 171-198), Brown & Wright (1972, *J. Zool.*, Lond., 167: 97-132), Claugher (1971, *Bull. Wld. Hlth. Org.*, 45: 855-858), Oberholzer, Brown & Van Eeden (1970, *Wetensk. Bydraes Potchefstroom Univ.*, B, 10: 1-58) and Wright (1971, *Phil. Trans. Roy. Soc. Lond.*, B, 260: 299-313).

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THE SYSTEMATIC POSITION OF *"STAGNICOLA (BAKERILYMNAEA) CUBENSIS"*[1]

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Abstract

The freshwater pulmonate snail family Lymnaeidae, one of the families of the so-called "higher limnic Basommatophora," has been divided in the past into a number of species-groups (i.e., genera or subgenera), which generally can be recognized by their distinctive shell features. F. C. Baker in 1928 (*The fresh water Mollusca of Wisconsin*, Pt. 1, Wisc. geol. & natur. Hist. Surv., p 264) dealt with generic and subgeneric taxonomy of the Lymnaeidae. Prime characters for distinguishing several of the taxa in his scheme were the number of cusps exhibited by the 1st lateral teeth of the radulae, and when radular teeth characters conflicted with shell characters in assigning taxonomic placement to taxa, he weighed the radular characters more heavily. For example, when species which by shell characters had usually been placed with *Galba* (=*Fossaria*) were found to have bicuspid 1st lateral teeth (a condition he considered restricted to *Stagnicola*) rather than tricuspid lateral teeth as characterize other *Galba* or *Fossaria* species, he moved the bicuspid fossarids to the genus *Stagnicola*, and made a new subgenus, *Nasonia* (a pre-occupied generic-group name later replaced with *Bakerilymnaea* by Weyrauch (1964, *Arch. Molluskenk.*, 93: 169)). The shell of *Stagnicola* s.s. was characterized by Baker (p 194) as "...large, with gyrate or plaited columella, with heavy impressed spiral lines..." The shell of *Nasonia* (=*Bakerilymnaea*) was characterized (p 195) as "...small, without columellar plait, surface without distinct spiral lines."

One of the species placed in the subgenus *Nasonia* is Lea's (1841) *"Limnaea bulimoides."* It has bicuspid lateral teeth similar to *Stagnicola* s.s., but has a small shell devoid of spiral sculpture and without columellar plait, similar in these respects to species normally assigned to *Fossaria*. Burch & Lindsay (1972, *Malacol. Rev.*, 5(1): 16-17) found that foot muscle antigens of *"S." bulimoides* showed complete immunological correspondence with antiserum prepared from foot muscle tissues of *Fossaria obrussa* (a species with tricuspid lateral teeth and typical fossarid shell), while strong "non-identity" reactions occurred when *"S." bulimoides* antigens were tested with other lymnaeid antisera, including antisera from 2 species of *Stagnicola* s.s. (*S. elodes* and *S. emarginata*). They therefore concluded that *"S." bulimoides* is a member of the *Fossaria* group, as characters of its shell would imply, rather than belonging to a special subgroup of *Stagnicola*, as characters of its radula led Baker to believe.

In spite of *Fossaria bulimoides'* taxonomic placement, the validity of the subgenus *Nasonia* (=*Bakerilymnaea*) rests on the relationships of its type species, which is Pfeiffer's (1839) *"Limnaea cubensis."* In order to establish this relationship in the present study we tested antigens of *"B." cubensis* (collected near New Orleans, Louisiana, U.S.A) with our various lymnaeid antisera, as well as undertaking an electrophoretic foot muscle esterase study of the species in question. These studies showed, as in the previous study of *F. bulimoides*, that *cubensis* is not closely related to *Stagnicola* s.s., but to *Fossaria*. Therefore, the validity of the taxon *Bakerilymnaea* is doubtful. However, if it is retained as a subgenus or section, it should be transferred to *Fossaria*.

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ELECTROPHORETIC TECHNIQUES IN MALACOLOGY: APPLICATIONS AND PITFALLS[1]

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Abstract

A review was presented on the applications and pitfalls of electrophoretic techniques for malacology. Applications were classified into 5 categories as follows: (1) Characterization of hemolymph proteins, (2) taxonomy, (3) biochemical pathology, (4) developmental biology, and (5) analysis and purification of specific substances.

[1] This study was supported in part by Research Grant AI-00513 and Training Grant AI-00046 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

To date, hemolymph from more than 2 dozen species of molluscs has been analyzed by electrophoresis (Table 1). Similarly, the technique has been employed by taxonomists, and species from more than a dozen genera have been studied (Table 2). The technique offers particular promise in resolving problems in biochemical pathology and in developmental biology.

Hazards and pitfalls inherent to the methodology of electrophoresis and in the interpretation of results were reviewed. Attention was directed towards the selection and quality control of matrices, factors influencing resolution, toxicity and hazards of apparatus and chemicals employed, and to errors in the handling of samples. In addition, artifacts leading to faulty interpretations of data were discussed. A selected bibliography, including more than 60 citations, on techniques and applications of electrophoresis to malacology was distributed to the participants.

TABLE 1. A summary of molluscan species having hemolymph proteins analyzed by electrophoretic techniques.

Species[2]	Technique[3]	No. Fractions	Reference
Gastropoda			
Prosobranchia			
Viviparus maleatus	PE	5	Cheng & Sanders, 1962
	CAE	5	Cheng, 1964
Littorina littorea	CAE	3	Cheng, 1964
Polynices duplicatus	CAE	3	Cheng, 1964
Nassarius obsoletus	CAE	4	Cheng, 1964
Oncomelania hupensis	CAE	1+[4]	Targett, 1963
Pulmonata			
Lymnaea stagnalis	CAE	1+[4]	Targett, 1963
Helisoma duryi normale	PAGE	15	Cheng, 1969
Helisoma trivolvis	CAE	1	Cheng, 1964
Planorbarius corneus	CAE	ng	Targett, 1963
Bulinus truncatus	CAE	ng	Targett, 1963
Bulinus tropicus angolensis	CAE	ng	Targett, 1963
Bulinus nasutus	CAE	ng	Targett, 1963
Bulinus globosus	CAE	ng	Targett, 1963
Biomphalaria sudanica tanganyicensis	CAE	ng	Targett, 1963
Biomphalaria pfeifferi ruppellii	CAE	ng	Targett, 1963
Australorbis glabratus	CAE	5	Targett, 1963
	PE	3-6	Wright & Ross, 1963
	PAGE	9-12	Michelson, 1966
	PAGE	17-20	Lee & Cheng, 1972
Australorbis nigricans	CAE	ng	Targett, 1963
Tropicorbis centimetralis	CAE	ng	Targett, 1963
Polygyra sp.	MBE	7	Deutsch & McShan, 1949
Agriolimax reticulatus	AGE/SGE/ PAGE	1-10	Bailey, 1971
Bivalvia			
Ostrea virginica	SGE	2	Woods *et al.*, 1958
Ensis directus	CAE	3	Cheng, 1964
Modiolus demissus	CAE	2	Cheng, 1964
Mytilus edulis	CAE	2	Cheng, 1964
Musculium partumeium	CAE	1	Cheng, 1964
Cephalopoda			
Loligo pealeii	SGE	2	Woods *et al.*, 1958

[2]Nomenclature as given by original authors.

[3]PE = paper electrophoresis; CAE = cellulose acetate electrophoresis; SGE = starch gel electrophoresis; PAGE = polyacrylamide gel electrophoresis; MBE = moving boundary electrophoresis

[4]Plus sign (+) signifies additional minor fraction noted on occasion, but number not given; ng = specific number not given.

TABLE 2. Summary of studies on the application of electrophoretic techniques to the taxonomy of medically important snails.

Study	Sample/Tech.[5]	Stained for	References
Compared hosts and non-hosts of schistosomes	wo/IME/AGE	Antigens	Tran van Ky *et al.*, 1962
Compared hosts and non-hosts of schistosomes	h/CAE	Proteins	Targett, 1963
Species and populations of *Bulinus* and *Biomphalaria*	e/CAE	Proteins	Wright & Ross, 1965
Diploid vs polyploid Bulininae	fm/PAGE	Proteins	Davis & Lindsay, 1965
Bulinus vs *Biomphalaria*	dg/SGE	Esterases/Phosphatases	Wright *et al.*, 1966
Bulinus africanus and *B. forskalii* species groups	e/CAE	Proteins	Wright & Ross, 1966
Species and populations of *Bulinus*	fm/PAGE	Esterases	Burch & Lindsay, 1967
Bulinus of Lake Malawi	e/dg/CAE-IME	Proteins/Esterases	Wright & Klein, 1967
Bulinus species groups	dg/SGE	Esterases	Wright & File, 1968
Oncomelania hupensis chiui populations	fm/PAGE	Protein	Davis, 1968
Semisulcospira population	fm/PAGE	Protein	Davis, 1968
Oncomelana hupensis nosophora field and lab. populations	fm/PAGE	Protein	Davis & Takada, 1969
Indian Lymnaeidae	fm/PAGE	Protein	Burch & Lindsay, 1969
African *Biomphalaria* and *Bulinus*	fm/PAGE	Enzymes	Coles, 1970
Oncomelania nosophora and *formosana*	cs/PAGE	Proteins/Enzymes	Michelson & DuBois, 1971
Neotropical biomphalarids and lymnaeids	dg/SGE	Esterase	Malek & File, 1971

[5]wo = whole organism, h = hemolymph, e = eggs, fm = foot muscle, dg = digestive gland, cs = crystalline style, IME = immunoelectrophoresis, AGE = agar gel electrophoresis; all other symbols as in Table I.

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ELECTROPHORETIC VARIATIONS IN FOOT MUSCLE ESTERASES IN POPULATIONS OF SOME AFRICAN *BIOMPHALARIA* SPECIES[1]

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Abstract

The purpose of this study was to investigate population differences in the cultures of *Biomphalaria* spp. derived from various parts of Africa, maintained in the Mollusk Division, Museum of Zoology, The University of Michigan. Disc electrophoresis was applied to foot muscle extracts from snails from 6 populations of *B. pfeifferi* from Liberia, Ethiopia, Kenya, Rhodesia and 2 sites in Tanzania, and 1 population each of *B. alexandrina* from Egypt and *B. sudanica* from Ethiopia. The 7.5% acrylamide gel columns were

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stained for non-specific esterases, then visually inspected and Rf values determined for each band by direct measurement. Densitometric tracings also were made so that corresponding peaks could be compared.

Biomphalaria pfeifferi, *B. alexandrina* and *B. sudanica* had 4 heavily stained bands: twin bands near the front, 1 in the middle and 1 near the origin. Variations were found between the populations and these were sufficiently consistent to distinguish the populations from one another. The main variable factors were the presence, absence or relative prominence of the 2 bands immediately behind the twin bands. Also, the band near the origin had 2 to 4 peaks in the Kenyan and the 2 Tanzanian populations, while it had only 1 peak in all others. Also, minor intra-population variations were observed in a few of the populations, but these were usually in terms of the relative prominence of certain of the peaks and did not unduly affect the characteristic pattern of each population.

It was observed that though on purely morphological grounds the populations of *B. pfeifferi*, *B. alexandrina* and *B. sudanica* were recognizable as distinct species, their esterase patterns indicated only minor variations, since both the *B. sudanica* and *B. alexandrina* populations, as well as the Rhodesian, Liberian and Ethiopian populations of *B. pfeifferi*, formed a progressive series with respect to the state of the 2 bands behind the twin bands.

Davis & Lindsay (1967, *Malacologia*, 5(2): 311-334), Wright & File (1968, *Comp. Biochem. Physiol.*, 27: 871-874) and Michelson (pers. comm., 1972) have pointed out that though esterase patterns can be relied upon to demonstrate population differences within a species, they are not necessarily equally reliable in evaluating relationships between different species. This is because, sometimes, interpopulation differences may even be greater than those between species. In fact, Malek & File (1971, *Bull. Wld. Hlth. Org.*, 45: 819-825), working with 15 populations of 5 species of *Biomphalaria* from South America, found a total of 5 esterase patterns which occurred in varying proportions in the different populations, irrespective of species.

Finally, workers on esterase patterns of *Biomphalaria* populations have tended to infer a correlation betweeen esterase patterns and susceptibility to infection with *Schistosoma mansoni* (e.g., Malek & File, 1971, *op. cit.*). It is recommended that a direct correlation could be drawn if an experiment is designed to infect individuals of various snail populations with different strains of *S. mansoni*, and then determine the degree of susceptibility and the actual esterase pattern of each snail and population.

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THE OCCURRENCE OF HEMAGGLUTININS IN SOME BASOMMATOPHORA AND STYLOMMATOPHORA[1]

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Abstract

An attempt was made to confirm the presence of hemagglutinins in hemolymph (H) and saline extracts of whole body (WB) or albumen gland (AG) of some basommatophoran and stylommatophoran snails.

Red blood cells (RBC) from the following were used: Human A, B, O, *Rana pipiens* (RP), brown Norway rat (BR), mouse (M), gerbil (G), rabbit (RA), dog (D), cat (C) and Rheuses monkey (MK). *Rana pipiens* RBC's were not tested against hemolymph. The *Bulinus* species were from populations maintained in the laboratory at the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan. All other species used were field collected specimens from Michigan. Tests were made on glass slides at room temperature (22°C).

The presence of hemagglutinins was confirmed in the following stylommatophoran snails: *Triodopsis multilineata*, A (AG); *Stenotrema leai*, A, O (AG); *Cionella lubrica*, A (WB). Hemagglutinins were not observed in the following: *Ventridens ligera* (AG), *Catinella vermeta* (WB) and *Oxyloma retusa* (WB). The basommatophoran snails *Physa integra* (WB), *Physa gyrina* (WB) and *Stagnicola elodes* (AG) did not show the presence of agglutinins. Various populations of *Bulinus* showed hemolytic activity in whole body extracts or the presence of agglutinins in the hemolymph. The presence or absence of hemolymph hemagglutinins in the various species of *Bulinus* varied from population to population. Also, individuals within a given population were not always identical in their reactions toward red blood cells. The results from the *Bulinus* populations are given in Table 1.

[1] This investigation was supported (in part) by grants AI-07279 and 5 T1 AI 41 (Training Grant) from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

TABLE 1. *Bulinus* hemolymph and whole body extracts

Population	Hemolymph	Whole body
Bulinus tropicus tropicus (n=18)		
1. Rhodesia	–	–
2. South Africa	–	–
3. Sinoia Road, Rhodesia	+ (MK)	–
4. Marlborough, Rhodesia	–	* (A, B, O, M, MK, G)
5. Shamva Road, Rhodesia	–	–
6. Kenya	Not done	–
Bulinus natalensis (n=18)		
1. Little England Farm, Rhodesia	+ (MK)	* (A, B, O)
2. Crocodile Creek, Rhodesia	+ (MK)	* (MK)
3. Fisherman's Bend, Rhodesia	–	–
4. False Creek, Rhodesia	+ (MK)	* (A, B, RA, MK)
5. Sulultu Road, Ethiopia	–	–
Bulinus truncatus truncatus (n=36)		
1. Sudan	+ (MK, C, G)	+ (MK)
2. Egypt	+(MK , C, G)	+ MK)
3. Dezful, Iran	+ (MK, C, G)	+ (M, RA, MK, C, G, BR)
Bulinus truncatus rohlfsi (n=36)		
1. Ghana	+ (C)	* (A, B, O, RA, MK, G)
2. Mauritania	Not done	–
Bulinus guernei (n=36)		
1. Gambia	Not done	–
Bulinus coulboisi (n=36)		
1. Tanzania	+ (MK, C, G)	Not done
Bulinus sericinus (n=36)		
1. Ethiopia	+ (MK, C, G)	Not done
Bulinus hexaploidus (n=54)		
1. Ethiopia	+ (MK)	Not done
Bulinus octoploidus (n=72)		
1. Ethiopia	+ (MK, G)	–
Bulinus (Physopsis) globosus		
1. Senegal	+ (MK)	Not done

+ Agglutination; – No agglutination; * Hemolysis

Numbers in parenthesis indicate haploid chromosome number

* * *

PIGMENTATION VARIATIONS IN *BIOMPHALARIA GLABRATA* AND OTHER PLANORBIDAE

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Abstract

Pigment has been used as a genetic marker in studies on the genetics of the host-parasite relation between *Biomphalaria glabrata* and *Schistosoma mansoni* (Richards, 1970, *Nature*, 227: 806-810; Richards & Merritt, 1972, *Amer. J. trop. Med. Hyg.*, 21: 425-434). This pigment character is determined by a

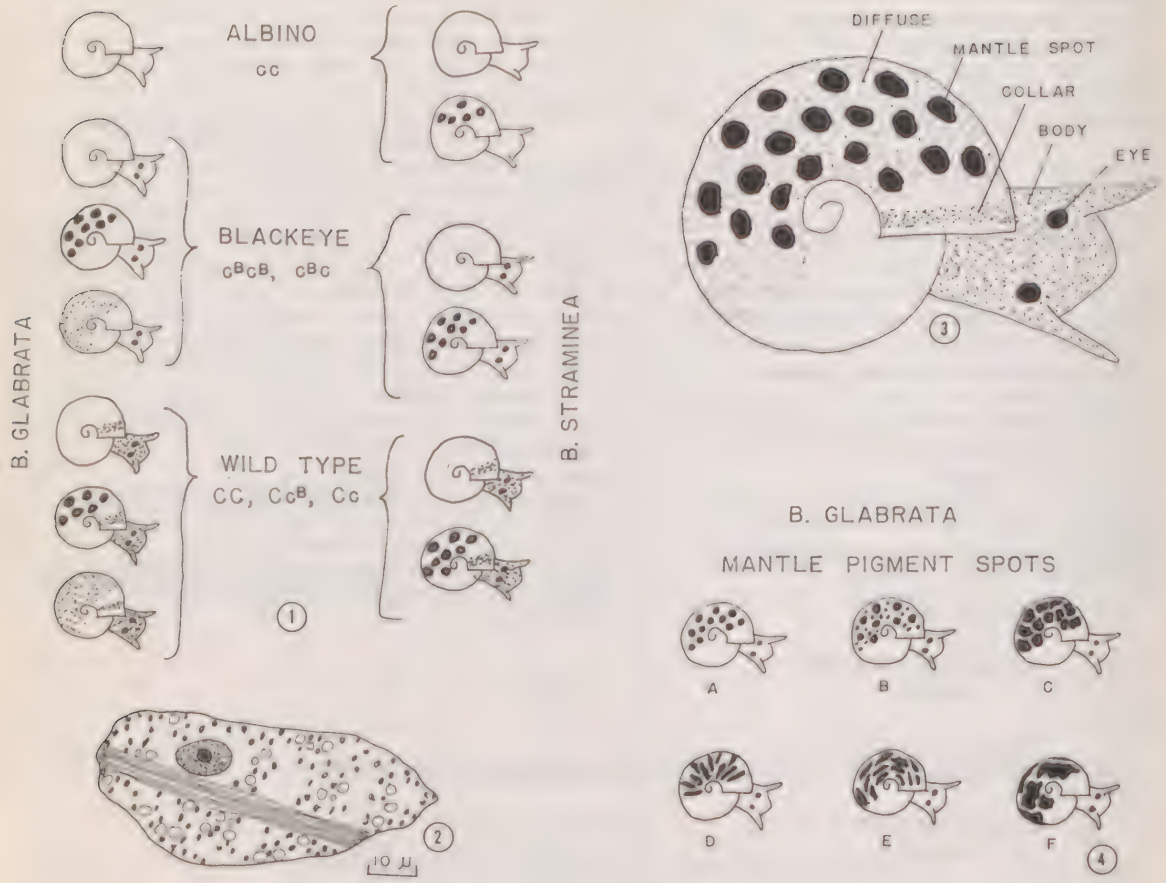

FIG. 1. Diagram showing the genotypes and phenotypes of the marker pigment character in *B. glabrata* and *B. straminea*, and mantle pigment variations observed. FIG. 2. Large pigment cell from connective tissue of *B. glabrata*, showing nucleus, pigment granules and bundle of needle-like inclusions. FIG. 3. Typical wild type *B. glabrata*, showing some of the types of black pigment. FIG. 4. Drawings of *B. glabrata* (blackeye) to show some of the mantle spotting patterns: (a) evenly spotted, (b) smaller spots interspersed between large spots, (c) irregularly shaped spots separated by narrow unpigmented channels, (d) transverse elongated spots, (e) longitudinal spots and (f) spots coalesced to form large black areas.

single gene and follows simple Mendelian inheritance (Newton, 1954, *Proc. helminthol. Soc. Wash.*, 21: 72-74). Three alleles of this gene occur in *B. glabrata* (Fig. 1). Wild type pigmentation, with black eyes and black pigment in body and mantle collar, is dominant. Albinism, with absence of black pigment, is recessive. Black eye pigmentation, deficient in body and collar pigment, is recessive to wild type but dominant over albino. Six possible genotypes occur expressed as 3 phenotypes, the use of which in genetic studies was described by Richards (1973, *Malacol. Rev.*, in press). In the course of these studies several kinds of pigmentation have been observed, some of which display qualitative and quantitative intraspecific and interspecific variation.

Hemolymph of planorbid snails is typically red due to occurrence of hemoglobins. Our clonal stocks of albino *Biomphalaria glabrata* range from consistently bright red to consistently pale pink. In several clonal stocks about 5-10% of the juveniles have colorless hemolymph, this deficiency in red pigment apparently being inherited.

Yellow-orange colored pigment granules, frequently rod-shaped, occur distributed throughout many of the tissues of *Biomphalaria glabrata* and other planorbids studied.

A large, specialized type of pigment cell occurs in the connective tissue of *Biomphalaria glabrata* and other planorbids (Fig. 2). These cells contain pigment inclusions ranging from pale straw through bright red to dark brown. Under adverse conditions these cells may become more numerous. Because of their

pigment and large size (the cell in Fig. 2 measured 30 X 70 μ) these cells can be distinguished individually with a dissecting microscope. In addition to a compact, round to oval nucleus and pigment inclusions, each cell in *B. glabrata* contains bundles of long, needle-like inclusions. Similar large pigment cells have been observed in all planorbids examined, but the needle-like inclusions have only been seen in *B. glabrata*.

The pigmentation employed as a genetic marker involves 2 of several types of black pigmentation (Fig. 3). In a typical wild type *Biomphalaria glabrata* the following black pigments may be recognized: black eyes, black pigment in body and mantle collar, discrete black mantle spots, diffuse mantle pigment, and a reticulum of black pigment cells lining the pulmonary cavity and the hemocele. The black pigment in the body and mantle collar consists of granules in cells in the connective tissues.

Mantle spotting results from groups of 1 to several adjoining epithelial cells containing a concentration of black pigment granules, absent or in lesser concentration in the surrounding epithelial cells (Richards, 1969, *Malacologia*, 9: 339-348). The pattern of mantle spotting is extremely variable in *Biomphalaria glabrata*, but within a clonal stock the pattern is usually consistent. Both degree and form of mantle spotting are inherited apparently as multifactorial characters. Fig. 4 illustrates some of the spotting patterns. Mantle spotting may occur in both wild type and blackeye *B. glabrata*. True breeding unspotted stocks of both pigment types were derived by selection. Although albino *B. glabrata* do not produce black pigment, they transmit the genetic factors for type of mantle spotting (Richards, 1969, *op. cit.*).

Diffuse mantle pigmentation results from scattered pigment granules throughout the epithelial cells. This pigmentation and the reticulum of black pigment cells lining the hemocele and pulmonary cavity vary in intensity, this variation apparently being inherited.

Genetics studies on susceptibility of *Biomphalaria straminea* to infection with *Schistosoma mansoni* have been initiated for comparison with *B. glabrata*. Pigmentation serves as a genetic marker. As in *B. glabrata*, a single gene, with 3 alleles, follows simple Mendelian inheritance (Fig. 1). As in *B. glabrata*, wild type is dominant, albino recessive, and blackeye recessive to wild type but dominant over albino. Diffuse mantle pigment has not been observed in *B. straminea*, but a reticulum of black pigment cells lines hemocele and pulmonary cavity. Wild type and blackeye *B. straminea* have been selected for presence or absence of mantle spotting, and when present, spotting shows a variety of patterns. Some *B. straminea*, offspring of albinos, have black mantle spotting but no other apparent black pigment. We have never observed mantle spotting in "albino" *B. glabrata*.

Many of the pigment variations seen in *Biomphalaria glabrata* have also been observed in other planorbids. In comparing *B. glabrata* with *B. straminea*, some pigment characteristics appear distinctive: the needle-like inclusions in the large pigment cells, and diffuse mantle pigment in *B. glabrata;* the mantle spotting in some "albino" *B. straminea*.

* * *

BREEDING EXPERIMENTS WITH *STAGNICOLA ELODES* AND *S. EMARGINATA*[1]

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Abstract

Systematics of lower taxonomic categories in the Lymnaeidae, especially those of North America, has always been difficult and often controversial. Especially bothersome is how to apply the species concept to the great amount of natural variation often found within and among populations, and how to delimit and describe species, races and populations in a meaningful and useful way. Also, a problem has been to decide whether or not valid species groups occur, and if so how to treat them. On the one hand are the "lumpers," who would tend to drastically reduce the number of taxa, usually without sufficient critical data, and on the other hand are the "splitters," who would finely divide the family into genera, subgenera, species and subspecies *ad infinitum*. What is needed, obviously, is more biological data that can be specifically used to make taxonomic evaluations. It is for that purpose that we conducted our cross-breeding studies on 2 critical lymnaeid populations (or species in traditional usage), *Stagnicola elodes* (Say) and *S. emarginata* (Say).

Typical *Stagnicola elodes* and *S. emarginata* are clearly and easily distinguishable. The former nearly always has a brown, elongate (high-spired) shell with relatively narrow body whorl, and the animal usually has a darkly pigmented body. Its habitat is in standing (or very slow-flowing), quiet, eutrophic waters. *Stagnicola emarginata* has a white (usually), grey or sometimes pale tan shell, which is globose, low-spired, and has a very large body whorl. The animal is pale, sometimes grey, but often seemingly totally without dark pigment of any kind. They live in lakes, usually large oligotrophic lakes with heavy wave

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action and sandy, gravel or rock bottoms. The specimens of both species used in our cross-breeding experiments were typical; in fact, these 2 species and populations were picked because of their contrasting and easily recognizable characters.

Specimens of both species were isolated as eggs or as very young snails (3 mm shell length or less) to preclude the possibility of their having mated with a sibling. They were raised to young adulthood in individual containers, then placed together with the opposing species as single mating pairs. After mating was observed, the 2 snails were separated again and maintained in isolation with careful records kept of egg masses laid and phenotypes of progeny. Similar records were kept for additional cultures in which mating was not directly observed, but considered highly probable, since mating was not a rare occurrence in the other cultures. F_1 individuals were isolated and mated with siblings to determine morphological characteristics of the 2nd (F_2) generation. The purpose of these studies was to determine whether individuals of these 2 populations (considered "species" in traditional usage) were interfertile or reproductively isolated. If they were found to be interfertile, producing viable, non-sterile and reproductively "normal" progeny, over several generations, then it would lend considerable weight to Walter's (1969, *Malacol. Rev.*, 2(1): 1-102) contention that these 2 populations are only variants of the same species, and perhaps even lend credibility to his drastic (p 5) stand "...that practically all of the nearly 60 species of North American '*Stagnicola s.s.*' recognized by F. C. Baker ought to be taxonomically united under the name *Lymnaea catascopium* Say." On the other hand, if these 2 populations are reproductively isolated, then it would indicate that lumping all *Stagnicola*'s under 1 species is an error, perhaps a gross one, and that critical biological studies such as we are attempting should form the basis of most, if not all, taxonomic changes.

In our studies we were unable to demonstrate cross-fertilization between any of our species pairs, although mating was frequently observed and nearly all individuals actively laid eggs, which hatched and grew into adults morphologically resembling in all ways their egg-laying parent. This was true for both 1st and 2nd generations. Since there was no evidence for genetic exchange between mating individuals of the 2 populations, even in the 2nd generation, it seems obvious that cross-breeding was not successful, and all progeny were the result of self-fertilization in these hermaphroditic animals. Consequently, unless further data suggests the contrary (e.g., that *Stagnicola elodes* and *S. emarginata* are near opposite ends of a "Rassenkreis"), then these 2 species should be considered taxonomically distinct. Not only are they readily distinguishable morphologically (and interfertility could not be demonstrated), but they live in quite different habitats. That they are not simply ecophenotypes can be demonstrated by laboratory culture. Each species has maintained its morphological characteristics for many years in our laboratory under identical conditions.

* * *

EMBRYONIC STRUCTURES IN THE EVALUATION OF INTRAPULMONATE RELATIONSHIPS

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Abstract

All orthurethran, sigmurethran and mesurethran snails so far investigated possess a well-developed podocyst during the stages of organogenesis. Although previous reports indicated camaenids lacked a podocyst, our investigation of *Varohadra yeppoonensis* indicates they have an unusually well-developed podocyst which may envelope the whole embryo at some stages. Heterurethran species all lack podocysts and have a general mode of development which is quite distinct from other stylommatophorans. Also, both the nervous system and kidney are distinctive in the succineids. From embryological evidence, one would judge the Heterurethra to be either a distinct line with affinities to the Basommatophora or intermediate between the Basommatophora and other Stylommatophora.

* * *

COMPARATIVE OBSERVATIONS ON SPECIATION IN TWO SPECIES OF PROSOBRANCHS, *GIBBULA CINERARIA* (LINNÉ) (TROCHIDAE) AND *LITTORINA SAXATILIS* (OLIVI) (LITTORINIDAE)

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Abstract

1 - Critical study on the relationships between *Gibbula cineraria* and *Cantharidus strigosus* (Gmelin). The problem concerning *G. cineraria* appeared to us when the late B. S. Kisch reported *C. strigosus* as a new species for the Basque coast. Having been consulted about the systematic place of this species, we established that, contrary to its shell, the radula of this species seemed to be like that of *Gibbula*. Later, the similarity with *G. cineraria* was evident (E. Fischer-Piette, J. M. Gaillard & B. S. Kisch, 1962, *Mém. Mus. natn. Hist. natur.*, n.s., 28, fasc. 1, 28 p).

Investigating populations from northern to southern Europe, we distinguished 3 areas: (1) from northern Europe to the south of France, (2) north coast of Spain and (3) northwestern Spain to Morocco. In the first area, from north to south, many morphological characteristics of the shells change step by step. The height/diameter ratio increases, and shells become more slender; but on the other hand, they remain smaller. The columellar tooth is more and more distinct and more and more frequent; the peribasal excrescence, always absent on those shells found on the English and French coasts of the Channel, appear on those forms from the south coast of Brittany but are never generalized in complete populations. The ornamentation of delicate lines is complicated with spots on those from southern localities, and the colour of these lines and spots changes from grey to lilac. Thus, many conchological characteristics change in parallel one with the other, from north to south. In the second area, the north coast of Spain, the progression is completely comparable but opposite. From east to west there is a progressive return to northern characteristics. Thus, in northwestern Spain, we found shells much as they are in Brittany. In the third area, from northwestern Spain to Morocco, the characteristics turn back. The changes, step by step, are the same as from northern Europe to the south of France. On the coast of Morocco, the "southern form" that received the name *Cantharidus strigosus* has developed all its characteristics.

Here, it is necessary to note a particularity in the manner in which the climate changes along the European coasts. The classic evolution from north to south is modified in the Bay of Biscay. In the southeastern part of the Bay, on the French and Spanish Basque coasts, the climate is unexpectedly warm. Thus, along the north coast of Spain, going westwards, we observe a climate more and more northern in character. And, in the most northwestern coast of Spain, in Galicia, the climate is somewhat similar to the climate of French Brittany. Thus, we point out an agreement between the gradual and successive changes of morphology of *Gibbula cineraria* and the gradual and successive changes of climate. This agreement applies, not only from north to south, but also with regional particularities in the climate of the Bay of Biscay. We have come to the conclusion that there exists only 1 species with characteristics changing in agreement with a climatic gradient. This continuity of morphological variation is quite probable for such a species, not only intertidal, but also subtidal, with eggs shed free and free-swimming trochophore larvae. Genetic exchanges between populations are thus possible, although the large geographic distribution of the species and the restricted life of pelagic phases forbid a complete mixing of characteristics while permitting dissimilarity between distant populations.

2 - Analytical study of intraspecific variability of *Littorina saxatilis*. Our second example is more complicated. *Littorina saxatilis* is an intertidal species found up to above the extreme high-water of spring tides. The uncommon variability concerning the height/diameter ratio, the general shape, the variability in the strength and design of the sculpture which is sometimes entirely lacking, the colouring with many tints and the variability or absence of lines was pointed out long ago. Recent observations have shown that the distribution of these characteristics in the populations of this species is extraordinarily variable, the degree of variability itself being also very different in each population (Fischer-Piette, Gaillard & James, 1963, *Cah. Biol. mar.*, 4: 1-22; Fischer-Piette & Gaillard, 1971, *Mém. Mus. natn. Hist. natur.*, n.s., 70: 1-89). To clarify the type of problems we are actually facing (Fischer-Piette, Gaillard & James, 1964, *Cah. Biol. mar.*, 5: 125-171), we need, first, to discuss in some detail the characteristics of 5 populations. Afterwards we will examine some statistical observations. The 5 localities we chose among our 617 stations are located in the marine part of Ria del Barquero, on the north coast of Spain, and are close to each other to avoid geographical difficulties. These localities are Punta Muinos, Puerto de Vares, Punta Castro Vilela, Punta Perveques and Playa Xilloy. Punta Muinos: All shells are smooth, grey greenish, not at all variable. Puerto de Vares: Shell more or less costulated; colour variability is important; ornamentation is typically composed of dark brown lines, more or less speckled, and white hyphens, more or less numerous, on a background colour of medium brown. Some specimens appear almost uniform with the progressive disappearance of the brown lines and scarcity of white hyphens. Punta Castro Vilela: All shells costulated; yellow, not at all variable. Punta Perveques: All shells costulated; there are 2 colour categories without any intermediates: 3/4 of the shells are yellow, 1/4 grey with a brown line in each groove. Playa Xilloy: All shells costulated; colour variability is very important:

69% are yellow, 4% orange, 2% have a brown line in each groove, 6% have all lines vanishing, 5% have brown lines vanishing in the equatorial sector, normally brown elsewhere, 4% have a brown speckled line in each groove, 4% have the grooves clearer than the crests and 6% have a brown line in clear grooves.

These 5 analyses give a good idea of the problem of intraspecific variability in *Littorina saxatilis*, although many other possibilities exist. We observe, first, homogeneous populations, but they are quite different in their sculpture and in their colour; secondly, we observe heterogeneous populations - in each of these, many coloured aspects are present with many intermediates; one of these populations, with its brown general colour, is very different from the polychrome population. Why do some phenotypes exist in some populations and not in others? The answer would seem to be that the ovoviviparity of the species and the absence of a pelagic phase almost completely eliminate the possibilities of dispersion and of mixing between neighbouring populations. It is a first element of isolation between populations. The conditions of intertidal life, particularly at high tidal level, divide the substratum into compartments and create a second element of isolation between populations. We observe, thirdly, a population with 2 varieties without any intermediates. Why do intermediate forms, with vanishing or speckled lines and present in neighbouring stations, not exist in this population?

A statistical study of 250 Spanish and Portuguese populations allows us to note that the distribution along these shores is not the same for all varieties. Some exist all along the shore, others are seldom present or even absent altogether in some regions (Fischer-Piette & Gaillard, 1971, *op. cit.*). Some colour varieties seem particularly frequent in certain types of stations. Their presence is more or less frequent, their abundance more or less great in parallel to certain ecological data (Fischer-Piette, Gaillard & Delmas, 1966, *Bull. Mus. natn. Hist. natur.*, ser. 2, 38: 874-897; Fischer-Piette & Gaillard, 1971, *op. cit.*). A study of the distribution of sculpture variation in some groups of stations in Spain and in France also indicates a relationship between exposure to waves or to currents and development of sculpture (Fischer-Piette & Gaillard, 1960, *J. Conchyliol.*, 100: 10-37; 1961, *Bull. Soc. zool. France*, 96: 163-172; Fischer-Piette, Gaillard & Jouin, 1961, *Bull. Soc. zool. France*, 86: 320-328). Thus, it seems that characteristics of coloration and costulation are in relation to physiological characteristics and that some morphological varieties can be considered as physiological varieties.

3 - Comparative observations. Our 2 series of observations about *Gibbula cineraria* and *Littorina saxatilis* are, at the same time, opposite but complementary. In the first example, *Gibbula cineraria*, many morphological characteristics were gradually changing in agreement with a climatic gradient. This continuity of morphological variation is easy to understand for such a species with a planktonic dispersal phase and probably few ecological barriers. Thus, although it has homogeneous local characteristics and important global variability, by virtue of genetic exchanges speciation does not really seem to be occurring. In the second example, *Littorina saxatilis*, 2 factors share in isolating populations from one another: first, the ovoviviparity of this species and second, the very particular amphibious environment, the discontinuities of the substratum and the ecological factors at high tidal level. The combined effects of these 2 categories of barriers almost completely eliminate genetic exchanges between populations which are evolving independently. As a result, we observe numerous forms, often poorly isolated one from another, difficult to define and associated in such a manner as to constitute populations whose aspect is still more variable and surprising. As in our first example, but only in limited cases, our provisional conclusions indicate some parallelism between environment and morphological characteristics. It appears that this global situation results as much from local genetic co-adaptation as from differential environmental selection. It seems, however, in this case too early to indicate to what degree speciation is acting positively.

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GENERIC AND SPECIFIC CHARACTERS IN THE LAND SNAIL FAMILY SUCCINEIDAE[1]

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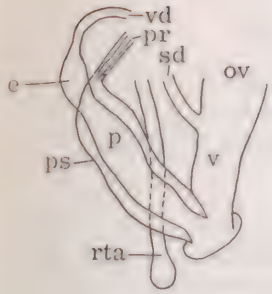
Abstract

The land snail family Succineidae exhibits a diversity of morphological characters in the reproductive tract which is the basis for generic distinctions. The generalized outline drawings below illustrate the characters of the reproductive tracts for the 9 major succineid genera I have studied (1 genus is not yet named). There are a total of 13 genera in the Succineidae, but only 10 have as yet been studied anatomically. Following the illustrations below is a list of morphological characters which should be useful in studies delineating species belonging to these 9 genera.

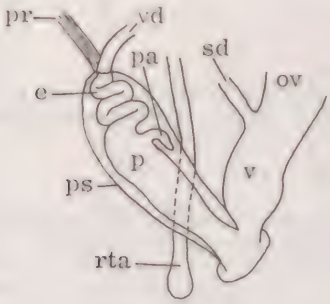
[1] This investigation was supported, in part, by PHS Training Grant No. 5 T1 AI 41 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

GENERIC AND SPECIFIC CHARACTERS OF SUCCINEIDAE

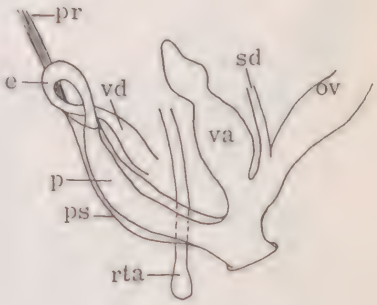
SUBFAMILY SUCCINEINAE
(penis with a penial sheath)



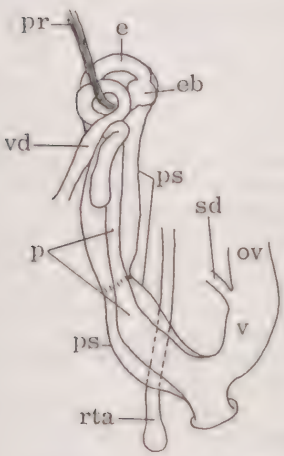
Succinea



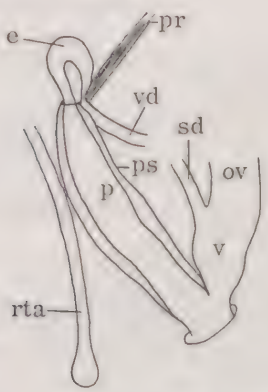
Oxyloma



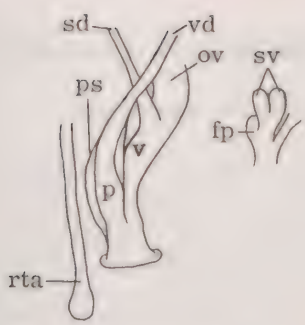
Neosuccinea



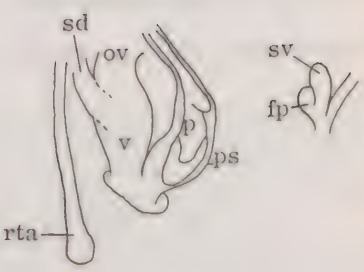
Omalonyx



unnamed genus

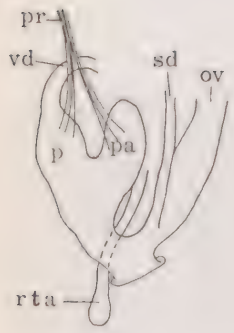


Indosuccinea

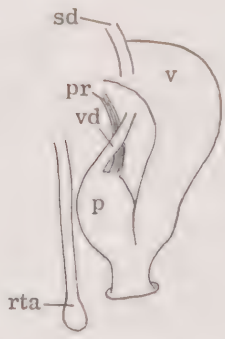


Lithotis

SUBFAMILY CATINELLINAE
(penis without a penial sheath)



Catinella



Quickia

KEY

rta	right tentacle assembly
p	penis
ps	penial sheath
e	epiphallus
vd	vas deferens
pa	penial appendix
pr	penial retractor muscle
v	vagina
ov	oviduct
sd	spermethecal duct
va	vaginal appendix
fp	fecundation pouch
sv	seminal vesicle(s)
eb	epiphallial bulb

Some characteristics useful in species identification

Shell- shape and size relationships
sculpture
color and relative thickness
Radula- number of teeth in a row and their morphology
number of rows
Pigmentation- color and pigmentation patterns both internal and external
Kidney- shape and color
Reproductive structures-
relative size of structures
shape and orientation of structures
insertion of penial retractor muscle and attachment of penial retractor muscle
length of vagina
relative length of spermathecal duct
thickness and number of muscle layers in penial sheath
type of penial sheath and whether it encloses the penis entirely, epiphallus entirely etc.
length and course of vas deferens
duct system and structure of prostate gland
size, shape and number of seminal vesicles
length and pigmentation of ovotestis duct
relative size of spermatheca
presence of specialized features such as crystals within the penis or terminal female tract

Other considerations: habitat, egg masses and general body plan and appearance

* * *

General Session

* * *

CYTOPLASMIC LOCALIZATION IN *BITHYNIA TENTACULATA* AND ITS INFLUENCE ON DEVELOPMENT

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Abstract

Eggs of the freshwater prosobranch *Bithynia* have a very small polar lobe at 1st cleavage, which is nearly free of yolk granules. After staining with methylgreen-pyronine, a very special cup-shaped cytoplasmic inclusion becomes visible in the lobe, which no longer stains after pretreatment with RNAse, indicating that it contains RNA. In electron micrographs this special cytoplasmic region can be seen to consist of small vesicles, surrounded by a double membrane (Dohmen, to be published). Already present in full-grown oocytes, it remains at the vegetal pole during maturation; at 1st cleavage it is shunted via the polar lobe to the CD-cell. At 2nd cleavage it suddenly disappears before the cleavage furrow separates the C- and D-blastomeres. After separation of the blastomeres at 1st cleavage the CD-cell produces eye, statocyst, shell and operculum; these organs are absent in AB-halves. When the AD-blastomere is separated from the BC-blastomere at 2nd cleavage these adult organs are found in both halves.

This difference between the developmental capacities of the blastomeres isolated at 1st and 2nd cleavage is probably related to the special cytoplasm of the polar lobe, which at 1st cleavage is shunted exclusively to the CD-cell. At 2nd cleavage it disappears and apparently is distributed to both the C- and D-cell, so that AD and BC after isolation have the same potentialities.

Although in *Ilyanassa* (Clement, 1956, *J. Exp. Zool.*, 132: 427-446) the developmental capacities of the blastomeres separated at the 2-cell stage are in general the same as in *Bithynia*, after 2nd cleavage the situation is quite different. In *Ilyanassa* the D-cell must always be present for adult structures to develop. This difference in developmental potentialities between *Bithynia* and *Ilyanassa* may be related to the different stages at which the morphogenetic factors, included in the polar lobe, are released. In *Bithynia* this has already occurred at the end of the 2-cell stage, since combinations with either the C- or D-cell develop adult structures, whereas in *Ilyanassa*, according to Clement (1962, *J. Exp. Zool.*, 149: 195-216), these structures do not develop after removal of 1 D at the 8-cell stage.

* * *

ULTRASTRUCTURAL DEVELOPMENT OF *ILYANASSA*'S SHELL GLAND

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Abstract

The ultrastructure of calcification in the embryo *Ilyanassa obsoleta* is currently being investigated. Embryos incubated in pasteurized sea water and kept at 18°C, were fixed for electron microscopy. The embryos were fixed for 2 hours in 2% glutaraldehyde in pasteurized, filtered sea water at a pH of 7.40, rinsed in 0.2M phosphate buffer and post-fixed in 1% osmium tetroxide in 0.1M phosphate buffer, pH 7.5, for 1 hour. This was followed by rapid dehydration in ethanol and embedding in Epon 812.

The shell gland begins as an ectodermal thickening which undergoes an invagination and then an evagination. At this time, an organic sheet appears to lift away from the gland and the first visible shell is formed. Under polarized light, 8-9 day embryos begin to exhibit crystalline birefringence, signifying calcification of the shell.

Electron microscopic investigation reveals that the tall, columnar cells of the shell gland have extensive apical microvilli, directly associated with the developing shell. These ectodermal cells are rich in glycogen rosettes, rough endoplasmic reticulum and Golgi, and contain abundant mitochondria with transverse cristae.

As the embryo matures, the organic sheet, covered by an external coat of loosely aggregated, periodically striated fibers, lifts away from the middle of the shell gland. At this time, the cells begin to change from a tall columnar to a low squamous appearance. At 8-9 days of development, deposition of the inorganic phase, $CaCO_3$, begins within this organic matrix. By the time the veliger hatches from the capsule, in about 17 days, the shell, operculum and 2 otocysts are heavily mineralized.

* * *

INTERNAL DEFENSE MECHANISMS OF *OCTOPUS DOFLEINI*[1]

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Abstract

In this study octopi were injected with living bacteria or colloidal carbon, and the clearance rates and sites studied. Like other molluscs, the octopus clears particles from its blood rapidly, and may do this in specialized tissues rather than by means of blood phagocytes. Later innoculations of bacteria are cleared no more rapidly than primary ones, and no humoral antibacterial agent could be found in octopus blood, even if the octopus had previously encountered the bacterium. For clearance to occur, the blood must be circulating.

* * *

THE ROLE OF GALACTOGEN IN PULMONATE SNAILS

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Abstract

This report presents suggested areas of future research and previously published results from this laboratory and others on the role of galactogen in (1) the successful development of pulmonate embryos and (2) the preparation of the adult snail for successful reproduction (egg-laying).

Concerning development. The snail embryo is a closed system, relying on endogenous sources for nutrition and energy. The zygote is bathed in the perivitelline fluid; this fluid is taken into embryonic cells and serves as the nutritive substrate for development (Raven, 1972, *In: Chemical Zoology*, p 170, Florkin & Scheer, eds., Academic Press, N.Y.). The fluid contains proteins and the polysaccharide, galactogen. Galactogen is metabolized during development of *Lymnaea stagnalis* (Horstmann, 1956, *Biochem. Z.*, 328: 342-347) or just after hatching in *Helix pomatia* (Horstmann, 1965, *Z. Biol.* (Munich), 115: 133-155). Galactogen is thus a major source of energy and carbon for biosynthetic processes. The enzyme system responsible for galactogen catabolism in embryos is still unknown. How the breakdown product, galactose, enters other metabolic pathways is being investigated.

Concerning the sexually mature snail. Galactogen is synthesized in the albumen gland from a UDP-D-galactose precursor (Goudsmit & Ashwell, 1965, *Biochem. Biophys. Res. Comm.*, 19: 417-422). The polysaccharide is synthesized and accumulates in globules within secretory cells in response to abundant food, moisture and warmth. This occurs whether in nature (in the spring) or in the laboratory (Nieland & Goudsmit, 1969, *J. Ultras. Res.*, 29: 119-140). Galactogen is a major component of the albumen (perivitelline) fluid, the albumen gland secretion which envelopes each egg as it passes down the hermaphroditic duct.

In the adult snail, May (1934, *Z. Biol.*, 95: 401-430) ascertained that *Helix pomatia* shows a seasonal pattern of accumulation and dimunition of both galactogen and glycogen. Galactogen is confined to the albumen gland, while glycogen is found in all tissues. Galactogen builds up in the spring when the snail emerges from hibernation and begins feeding. In summer, the amount drops sharply as galactogen, the secretory product, is transferred to the eggs as part of their albumen layer. No more galactogen is synthesized until the next egg laying season. Glycogen accumulates prior to winter hibernation and is slowly utilized during that period. May also found that during starvation, although glycogen is depleted within 10 days, the galactogen reserves remain untouched. Galactogen is utilized as an emergency food reserve only after all the glycogen has been used up. Thus it appears that glycogen is the immediate energy source in the adult snail, while galactogen is not normally metabolized but is held in reserve for its role in egg laying.

Galactogen and glycogen are found in the same snail, and sometimes in the same cell (Nieland & Goudsmit, 1969, *op. cit.*). UDP-D-glucose and UDP-D-galactose are precursors in glycogen and galactogen synthesis respectively. These 2 sugar nucleotides are interconvertible via 2 routes; epimerase and nucleotidyl transferase. These enzymes are present in cell-free extracts of albumen gland (Goudsmit, 1972, *In: Chemical Zoology*, Florkin & Scheer, eds., Academic Press, N.Y.).

The factors governing biosynthesis of the parallel polysaccharides galactogen and glycogen within the snail would give a fascinating insight into control mechanisms. Thus the biochemical factors which may

trigger the synthesis of galactogen in response to spring-like conditions are unknown. Also unknown are the hormonal or enzymatic regulator molecules that stimulate glycogen synthesis and accumulation in preparation for winter hibernation.

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ORGANIC CONTENT OF EGGS AND JUVENILES OF AN AMPHIBIOUS SNAIL, *POMACEA URCEUS* (MÜLLER), FROM THE VENEZUELAN SAVANNAH AND THEIR ECOLOGICAL SIGNIFICANCE

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Abstract

The eggs of *Pomacea urceus* have white calcareous shells and have been observed in clutches of 50 to 200 beneath females with shell lengths ranging from 85 to 135 mm. Oviposition is at the beginning of the dry season, mainly in December-January after the female has burrowed into the surface mud. The spat hatch in January and aestivate beneath the female in the brood chamber until the next rainy season, 4 to 5 months later. Samples were taken in the plains (Los Llanos) near Camaguán, Venezuela. Eggs and spat were analyzed for total organic carbon using a wet oxidation method.

For 22 eggs, the mean diameter is 11.5 mm with a range of 6.7 to 15.5 mm. For 5060 spat, the mean shell length is 10.5 mm with a range of 5 to 15 mm. At the beginning of the dry season eggs and spat of mean size have 20.00 and 17.97 mg C respectively. This indicates a gross developmental efficiency [GDE = (100 x energy content of hatched animal)/(energy content of hatched animal + energy lost during development)] of greater than 89.9%. For most animals GDE is usually of the order of 60%.

Eclosion for some snails is undoubtedly early. These "early" spat probably proceed to feed upon the remaining eggs and thus abort others in the clutch (newly hatched spat readily feed upon fresh eggs provided in the laboratory). Some aborted snails apparently die. This could account for the high but unlikely GDE reported above. During the dry season (period of aestivation) spat of mean size (17.97 mg C at start) lose 40% or more (7.2 mg C) of their organic content. The production of large eggs and early eclosion of some snails is of selective advantage for survival through the long dry season. Many adults die before the end of the dry season and the spat survive in the brood chambers beneath the dead females. Spat become active within 3 minutes to an hour of submersion in water. These fully developed juveniles are therefore assured an opportunity to fully exploit the favorable conditions for growth throughout the rainy season. This is important since a minimum adult size of at least 85 mm shell length is evidently necessary for aestivation. The efficiency of reproduction not only involves absolute energy values, but also the timing of reproduction in relation to seasons and life history.

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ACTIVITY PATTERNS OF *LYMNAEA STAGNALIS* (L.) IN RELATION TO TEMPERATURE CONDITIONS: A PRELIMINARY STUDY[1]

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Abstract

The rapidly expanding use of rivers and lakes for domestic and industrial uses is artificially warming the surface waters of many countries. In general, research on the effects of thermal loading on organisms has dealt with distribution, relative abundance and physiological responses. A neglected area is that of behavioural responses. The purpose of this study is to ascertain the behavioural responses of the cold water snail *Lymnaea stagnalis* (Linnaeus) to increased sublethal temperature regimes. As a 1st step to interpreting these behavioural responses, diurnal activity patterns were analyzed at a "normal" temperature of 20°C and a sublethal elevated temperature of 30°C. The variables measured were temperature, oxygen content, barometric pressure and food supply; the light regime was 12 hours light - 12 hours dark. Ten snails were maintained at 20°C for 7 days and the temperature was then increased 1°C/hour to 30°C at which temperature the snails were maintained for an additional 6 days. Throughout these 14 days, the activities of the snails were recorded on time-lapse film at the rate of 1 frame every 30 seconds. The preliminary results are based on detailed analysis of 3 of these snails at 2 days of each temperature regime. Among the results suggested by this analysis are that increased temperature (1) increases the rate of surfacing for breathing, thus (2) decreasing the time available for feeding, (3) does not alter the percentage of time spent in actual motion, but does (4) accelerate the rate of change of activity patterns and (5) induces a rhythmicity to certain of the activity patterns.

[1]Supported, in part, by PHS Training Grant No. 5 T1 AI 41 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

THE EFFECTS OF TEMPERATURE ON GROWTH AND REPRODUCTION IN AQUATIC SNAILS[1]

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Abstract

Abrahamson (1972, *In: The careless technology*, Doubleday/Natural History Press, Garden City, New York, p 795-811), Cairns & Scheier (1962, *Notulae Naturae*, (353): 1-12), Cairns (1972, *In: The Careless Technology*, *op. cit.*, p 829-853) and others stressed the need for studies designed to determine the effects of widespread development in the use of nuclear power reactors, either built or projected, in proximity to rivers and lakes in our country. Abrahamson, in discussing the ecological hazards from nuclear power plants, stated: "Over two-thirds of the total heat generated by a nuclear power station is discharged as waste into the local environment. Should this heat be introduced into lakes, rivers or estuaries, serious and widespread changes can be expected."

With the assistance of The Water Quality Office of the Environmental Protection Agency, the effects of temperature on the growth and reproduction of several freshwater snails was studied. The snails stressed were 2 lymnaeids (*Lymnaea stagnalis* and *L.* (*Stagnicola*) *emarginata*), 3 planorbids (*Helisoma trivolvis*, *H. anceps* and *H. campanulatum*), 1 physid (*Physa gyrina*) - all freshwater pulmonate snails; it was also possible to test 1 gill-breathing operculate (*Amnicola limosa*). Both growth and egg-laying were measured in temperatures maintained at intervals between 6°C and 36°C. The gonad development was studied with the use of paraffin sections and stained with haematoxylin and eosin; the reproduction was measured in terms of egg-laying.

Each of the 7 species was stressed in aquaria maintained at 6°, 12°, 18°, 24°, 30° and 34 or 36°C. The range varied with the groups, but none could be cultured much below 12°C and none would reproduce when the temperatures exceeded 30°C. While growth usually was better in "warm" water, the advantages were generally offset by a lack of proper gonad development. It appears that mollusks, like many animals cited, are quite sensitive to ambient temperatures. Even small changes in the environment may be important to the animals affected.

Figures given on the amounts of heated waste water that will return to a river, estuary, ocean or lake are astounding. The elimination of species will depend on their sensitivity, and we have now just begun to measure how sensitive some of them are. The problem is compounded because the higher temperatures in water make less dissolved oxygen available to the aquatic animals. In view of these conditions, field survey work deserves far more encouragement than it is receiving. Such studies should be both qualitative and quantitative and should serve to predict the probable changes heated waters would produce.

From the experiments carried out and cited in this report, while the snails grew well in water warmer than usual, they often failed to reproduce. The acclimatization shown could remove the normal occupants such as lymnaeids and allow the establishment of conditions that might favor planorbids like *Biomphalaria*, which can serve as intermediate hosts for schistosomiasis. More studies are needed especially with the operculate, gill-breathing snails for which there was not sufficient time in this project. Not only are freshwater snails widespread and common but, in terms of biomass, they are far superior to insects which have been considered as indices of heat pollution.

The role of many mollusks for determining the ecology during the past, the present and the future deserves far more attention than it has hitherto received. Additional studies which should receive immediate interest involve the following items:

1) More "plop" tests are needed to understand the levels of tolerance to sudden temperature changes among such a large and prominent group as the mollusks.

2) Too little is known, as yet, about the effects of temperature on the gill-breathing operculate snails (e.g., the pleurocerids, viviparids, amnicolids, etc.).

3) Trematode infections are often regulated by temperatures to which their mollusk hosts are subjected. Studies have been initiated in our laboratory in this field, but additional work is needed to determine the effects of temperature on the development of the parasites in their intermediate hosts.

4) Heat pollution caused by thermal reactors in rivers and lakes often produce "blooms" of algae. Since freshwater mussels are natural filtration agents and are often found in large populations in affected areas, tests should be made to determine how effectively they could serve in reducing algal growth.

5) The behavior patterns of mollusks are closely related to ambient temperatures. It is necessary, therefore, not only to ascertain their ability to withstand sudden changes (as in the "plop" tests), but to learn how they orient themselves under normal and abnormal temperature stress. A neglected area of research is that of the effect of thermal stress on behavior: on the rate of change of activity patterns (i.e., movement, respiration, feeding), alterations in copulation and egg-laying, and changes in horizontal and vertical migrations. Especially needed are studies dealing with the effects of short-term (i.e., hours) and long-term (i.e., days) thermal stress on behavior, as well as studies comparing the effects of fluctuating as opposed to constant elevated temperatures.

[1] The full report on which this abstract is based is currently in press as an Environmental Protection Agency publication under the sponsorship of the Water Quality Office.

A BRIEF REVIEW OF THE SYSTEMATICS OF THE FAMILY PHYSIDAE[1]

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Abstract

The Physidae, a family of commonly occurring freshwater pulmonate snails, are differentiated from other limnophilic basommatophoran snails by having the combination of (1) a sinistral shell, (2) V-shaped radulae and (3) the absence of hemoglobin. The family consists of 2 genera: *Aplexa* and *Physa*. *Aplexa* is differentiated from *Physa* by having a more elongate shell and lacking mantle digitation.

Subgeneric groupings based on the shell are summarized in Zilch (1959-60, *In:* Schindewolf, *Hand. Palläozool.*, Lief. 1-4, 6: 834 p, Borntraeger, Berlin). *Aplexa* is conventionally recognized as consisting of 2 subgenera, *Aplexa* s.s. and *Stenophysa*, while *Physa* consists of 4 subgenera, *Physa* s.s., *Alampetista*, *Costatella* and *Petrophysa*. These subgeneric groupings are at present of doubtful validity, since shell characters are known to be of little systematic value within the Physidae. Radular features similarly have proved to be of little use.

F. C. Baker (1928, *The fresh water Mollusca of Wisconsin*, Pt. I., Wisc. Geol. & natur. Hist. Surv., Bull. 70(1): 507 p) has proposed the regrouping of the American *Physa* species into 2 groups based on differences in the gross morphology of the male genitalia, one group having a long penial sheath with a constriction, the other group having a shorter penial sheath without a constriction. Clampitt (1970, *Malacologia*, 10: 113-152) has subsequently verified this trait and suggested that Baker's subgeneric divisions are basically sound. The validity of Baker's emendation of Haldeman's (1842, *In: A monograph of the freshwater univalve Mollusca of the United States*, Physidae, 40 p, Dorsey, Philadelphia) names *Physella* and *Physodon* for the 2 groups has been contested by Clench (1930, *Occ. Paps., Soc. natur. Hist. Boston*, 5: 301-315).

At present only 17 nominal species of the genus *Physa* have been described in regard to the penial sheath trait. Baker (1928) examined 11 species, Clampitt examined another 5 species, and Richards (1964, U.S. Dept. of Hlth., Educ. and Welfare, *Publ. Hlth. Rep.*, 79(11): 1025-1029), in his studies on Puerto Rican Physidae, showed *P. cubensis* to have the *"Physodon"* trait. I have examined 15 specimens of *P. gyrina hildrethiana* from several localities and 8 specimens of *P. parkeri* from Douglas Lake, Michigan, all of which showed consistently the reported *"Physella"* trait. The 21 specimens of *P. integra* from several localities that I examined likewise showed consistently the reported *"Physodon"* trait.

In addition to the above confirmation, I have these new reports to make. Specimens that I examined of *Physa virgata* from New Mexico, as well as *Physa* (spp.) specimens from France, Egypt and Ethiopia, all had male genitalia with unconstricted penial sheaths similar to the *"Physodon"* type.

Aplexa has a very different male genitalia morphology, as evident from a number of reports and in a number of my own dissections. When more detailed studies are done, this fact should be added to the number of diagnostic characters which at present differentiate *Aplexa* from *Physa*.

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APPARENT HYBRIDS FROM A LABORATORY CULTURE OF *LYMNAEA STAGNALIS* AND *BULIMNEA MEGASOMA*[1]

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Abstract

During the course of our taxonomic investigations on various species of the freshwater basommatophoran family Lymnaeidae, we maintained together in the same aquarium 2 North American species of this common, world-wide snail family: *Lymnaea stagnalis appressa* (Say) and *Bulimnea megasoma* (Say). These 2 species are the largest in their family, but apart from their similar size, the 2 are quite different in shell morphology.

[1]Supported, in part, by PHS Training Grant No. 5 T1 AI 41 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

Both species were collected from the field on the same day and maintained continuously in a single tank. Soon after they were brought to the laboratory and placed in an aquarium, egg masses appeared which subsequently hatched. As the young snails developed, it soon became apparent that their shells exhibited morphological traits of both species in the tank. These intermediate shells had the appearance of hybrids, as though they were the result of successful mating of the 2 snail species. If this were so, it would have been of special interest to us because our current research program uses hybridization techniques as taxonomic tools for species discrimination. *Lymnaea stagnalis* and *Bulimnea megasoma* have always been considered specifically distinct, and usually have been assigned to different generic or subgeneric groups. Their lack of reproductive isolation would be unexpected.

In order to further study these interesting lab-raised offspring, we turned to 2 biochemical techniques, electrophoresis of foot muscle non-specific esterases and immunology of foot muscle antigens, procedures which have been used for a number of years in our laboratory (e.g., see Davis & Lindsay, 1967, *Malacologia*, 5(2): 311-334; Burch & Lindsay, 1970, *Malacol. Rev.*, 3: 1-18).

Lymnaea stagnalis and *Bulimnea megasoma* each have clearly distinct electrophoretic foot muscle esterase patterns, and each is immunologically distinct, having detectably different foot muscle antigens. The electrophoretic esterase pattern of the phenotypically intermediate offspring were identical to that of *B. megasoma*. The offspring foot muscle antigen was immunologically indistinguishable from that of *B. megasoma*, but strong "non-identity" precipitin reactions occurred between offspring antigen and *L. stagnalis* antiserum, similar or identical to the reactions observed between *B. megasoma* antigen and *L. stagnalis* antiserum.

The next step will be to study the 2nd generation offspring. However, previous studies on hybrid esterase patterns indicate that F_1 hybrid offspring combine the esterases of both parents (e.g., see Wu, 1972, *Malacol. Rev.*, 5(2): 95-164). Since such a combination of esterase patterns was not observed in our 1st generation offspring, we do not expect to see any segregation of esterase patterns in the 2nd generation.

The evidence from our biochemical studies indicates that the offspring in our tanks, although appearing on shell characters to be true hybrids, are no more than variants of *Bulimnea megasoma*, probably the result of their artificial environment (i.e., they are "ecophenotypes"). That their ecophenotypic appearance grades towards conchological traits exhibited by *Lymnaea stagnalis* would seem to be fortuitous. Nevertheless, it points to the danger of making assumptions about seeming intermediate phenotypes of species maintained together in artificial environments.

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BULINUS SERICINUS (GASTROPODA: PLANORBIDAE) FROM ETHIOPIA[1]

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Abstract

Bulinus sericinus (Jickeli 1874) was the 1st planorbid bulinine snail to be named from the Ethiopian highlands. Burch (1969, *Malacol. Rev.*, 2: 113-114) showed that it is tetraploid (n=36, 2n=72), having twice the number of chromosomes found in most members of the Planorbidae (x=18). In this way, *B. sericinus* is similar to *B. truncatus* (Audouin 1827) of the Near East and Africa north of the Sahara, which is also a tetraploid species (Burch, 1964, *Malacologia*, 1: 387-400) and, incidentally, the intermediate host of human schistosomiasis in much of its area of geographical distribution. The present study compares the morphology of *B. sericinus* to that of its better known neighbor to the north, *B. truncatus*. The population of *B. sericinus* studied was a laboratory-bred stock from the type locality of the species, the Toquor River at Mekerka, Ethiopia. The *B. truncatus* specimens used for comparison were also a laboratory-bred stock, originally from Iflaka Bilharzia Project area, Behaira Province, Egypt.

In general, the morphology of *Bulinus sericinus* is the same as that of *B. truncatus*. The differences between the 2 species are listed below.

(1) The shells of *B. sericinus* were medium-spired (mean L/AL = 1.39)[2], had elongate-ovate apertures (mean AL/AW = 1.9)[2] and body whorl contours that were not markedly inflated. The shells of *B. truncatus* were high-spired (mean L/AL = 1.52), had ovate apertures (mean AL/AW = 1.68) and body whorl contours that were markedly inflated.

(2) The mantle pigmentation of *B. sericinus* was dark grey to black in irregular patches over a greyish background, and the tunica propria of the visceral hump was transparent, except for the area overlying the ovotestis. Neither the mantle nor the tunica propria of *B. truncatus* was pigmented.

(3) Five out of 64 *B. sericinus* radulae showed an asymmetrical development of the rachidian cusps,

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[2] L/AL, shell length/aperture length; AL/AW, aperture length/aperture width.

while 38 out of 150 *B. truncatus* radulae showed the rachidian cusp deformity with either 1 or both cusps missing.

(4) The numbers of lateral teeth of *B. sericinus* were always greater than those of *B. truncatus* of equivalent shell lengths.

(5) Reproductive maturity (using the initial enlargement of the seminal vesicle as an indicator) of *B. sericinus* occurred at 6.8-7.0 mm shell length, while that of *B. truncatus* was attained at 4.6-5.0 mm shell length.

(6) The percentage of euphallic specimens was low (1.8%) for *B. sericinus*, while it was high (15.2%) for *B. truncatus*.

Experimental infections of *Bulinus sericinus* with the Egyptian strain of *Schistosoma haematobium* were 52.6% positive, while Lo's data (1972, *Malacologia*, 11: 225-280) on experimental infections of *B. truncatus* with the same parasite strain showed only 3% positive. Cross-breeding of *B. sericinus* with a diploid albino strain of *B. tropicus* showed that 1 of 3 experiments succeeded in producing vigourous but sterile F_1 progeny, while none of 4 *B. truncatus* mated with the same albino succeeded in producing F_1 progeny. Electrophoretically separated foot muscle esterases of both *B. sericinus* and *B. truncatus* were identical. The foot muscle antigen of *B. sericinus* tested against antisera for *B. truncatus* showed no 'non-identity' precipitin reactions.

Because of the close morphological similarities between the 2 populations, *Bulinus sericinus* might well be only a race of *B. truncatus*. Cross-breeding studies may shed further light on this suggestion.

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ON THE DISTRIBUTION OF UNIONIDAE IN THE SYDENHAM RIVER, SOUTHERN ONTARIO, CANADA

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Abstract

Field experience by H. D. Athearn in 1963 and Dr. Carol B. Stein in 1965 and 1967 has shown that the unionid fauna of the Sydenham River is remarkably diverse. Further investigation seemed desirable, and therefore the writer and Louise R. Clarke collected specimens and performed water analyses on the river between August 21 and 25, 1971. Eleven stations were visited, their localities ranging from the headwaters to near the mouth. Some of the basic data obtained, including those from the August 4, 1963 collection of Athearn (Sta. 552), are condensed and summarized below.

Sydenham River water is hard and all stations gave hardness values between 170 and 270 ppm (as $CaCO_3$). The region of greatest species diversity begins about 10 miles southwest of Strathroy where the river first attains what may be "critical size," i.e., a width of about 50 feet. Local ecological conditions (sediments, current, etc.) influence local species composition, but diversity in general continues high downstream to near the town of Dresden, a distance of about 60 miles. Below that point no unionids were found.

The Lake Erie-Lake St. Clair drainage basin contains by far the richest unionid fauna in Canada. Within that region the molluscan communities of the Sydenham River appear to be the most natural and least disturbed. Every effort must be made to ensure their continued healthy survival.

TABLE 1. Collecting stations and ecological data*

Sta. No.	Location (headwater to mouth sequence)	Width (est. ft)	Current (est. mph)	Bottom	Vegetation abundance	Apparent Pollution	Time spent (hrs)
1040	2.7 mi SE of Ilderton	5-10	0	S, M	A	none	1.0
1041	2.6 mi NE of Coldstream	10	0	M	0	cows	0.7
1042	0.5 mi NNE of Coldstream	20-25	1	M, S	0	none	1.2
1043	2.2 mi NE of Strathroy	20-30	2	MS	0	none	1.0
1044	10.0 mi SW of Strathroy	50-60	2	SM	S	none	1.5
1045	3.0 mi NE of Alvinston	60-75	3	G, MS	0	none	1.5
1051	3.7 mi S of Alvinston	75	1	G, M	S	none	1.8
1050	3.4 mi NE of Shetland	75	1	M	S	none	1.0
552	1.8 mi NE of Shetland	75	-	R, S	-	none	4 ±
1046	0.4 mi S of Croton	100	1	M	M	none	1.0
1049	0.5 mi N of Dawn Mills	75-100	2	M, G	0	none	1.2
1048	1.0 mi W of Tupperville	150	1	M	S	indust.(?)	0.7

*Abbreviations. Bottom; G, gravel; M, mud; MS, muddy sand; R, rocks; S, sand; SM, sandy mud. Vegetation abundance: A, abundant; M, moderate; 0, none; S, sparse.

TABLE 2. Species and subspecies collected

Species and subspecies	Station numbers											
	1040	1041	1042	1043	1044	1045	1051	1050	552	1046	1049	1048
Fusconaia flava					+	+	+		+	+	+	
Quadrula quadrula									+	+		
Q. pustulosa										+		
Cyclonaias tuberculata						+	+		+		+	
Amblema plicata					+	+	+	+	+	+	+	
Pleurobema coccineum					+	+					+	
Elliptio dilatata						+	+		+	+	+	
Alasmidonta calceola			+									
A. marginata						+	+		+		+	
Lasmigona complanata					+							
L. compressa					+							
L. costata					+	+	+	+	+		+	
Anodontoides ferussacianus	+			+								
Anodonta grandis	+		+		+	+		+	+	+		
Strophitus undulatus					+	+			+			
Ptychobranchus fasciolaris						+	+		+		+	
Truncilla truncata										+		
Proptera alata										+	+	
Obovaria subrotunda					+	+	+					
Leptodea fragilis					+		+	+	+	+	+	
Actinonaias carinata						+	+		+	+	+	
Ligumia recta					+	+	+		+		+	
Lampsilis fasciola						+						
L. ovata ventricosa					+	+			+	+	+	
L. radiata siliquoidea					+	+	+	+		+		
Villosa fabalis									+			
V. iris						+			+		+	
Dysnomia torulosa rangiana									+			
D. triquetra									+			
Totals	2	0	2	1	13	17	12	5	18	12	14	0

* * *

A CASE FOR PROTECTING THE DRIFTLESS AREA OF THE UPPER MIDWEST

M. J. Imlay

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Abstract

In the Driftless Area of southeastern Minnesota, southwestern Wisconsin, northeastern Iowa and northwestern Illinois at least 4 likely endangered species of clams and snails still survive. This is the famous Northern Area, about 150 miles in diameter, that the 4 recent ice ages did not significantly demolish with their great glacial drifts. Other than by visiting this spectacular northern area, one must travel several hundred miles south to find areas with ancient dendritic patterned drainages, low mosquito counts and tall conical outliers of deep valleys.

One of the endangered mollusks (see Stansbery, 1971, *In: Proc. Symp. Rare and Endangered Moll. of U.S.*, U.S. Dept. Interior, p 5-19) is the freshwater mussel, *Cumberlandia monodonta*, commonly known as the Spectacle Case. This is the only species in an ancient genus which has more poorly-developed hinge teeth than most modern mussels (hinge teeth serve to avoid the shearing action of spring torrents that tend to tear the 2 shell valves apart). This species also appears to have more protein than other mussels in its shell composition. It inhabits firm mud and quiet water (possibly due to its rather fragile nature), but is stationed very near rapid water (because of heavy respiratory requirements) (see Stansbery, 1966, *Amer. malacol. Union, ann. Reps.*, p 29-30). *C. monodonta* was found in the Driftless Area (Baker, 1928, *The fresh water Mollusca of Wisconsin.* Pt. 2, Wisc. geol. & natur. Hist. surv., p 48-49) at Prairie du Chien. The nearest known population to this one is several hundred miles further south. Fortunately for

this species, instead of building a dam on the Mississippi River for flood control at Prairie du Chien, the Army Corps of Engineers has decided to relocate 157 old buildings.

Hendersonia occulta is a flood plain land snail species in the Driftless Area that is likely to become threatened with extinction according to J. P. E. Morrison (pers. comm., 1972). Found in the Kickapoo Valley, this conspicuous red snail is threatened by a dam that will inundate a full 1/3 of the best part of the Kickapoo Valley. Commonly known as the "Wild Cherrystone Snail," the rarity of this helicinid operculate was noted some years ago by Morrison (1929, *Nautilus*, 43(2): 41-45). The northern existence of a member of the Helicinidae, a predominantly tropical family, is a zoogeographical anomaly, and unfortunately, *H. occulta* has recently been decreasing in northern areas. On July 2, 1972, Dan Engstrom and I found *H. occulta* in the upper reaches of the area to be inundated by the dam. It was abundant on a slope under leaves in a dark sombre cave-like waterfall area known as Ice Cave, which is located in the lower part of Wild Cat Mountain State Park. On the same day we also found *H. occulta* at the east side of Devils Lake, Wisconsin, on a slope at the base of a talus fall, thus confirming an earlier find there by Morrison (pers. comm.). Situated at the edge of the Driftless Area, the spectacular valley of Devils Lake is a nonglaciated remnant of the old bed of the Wisconsin River. The lake is located at Devils Lake State Park, an intensive use recreation area.

Zonitoides limulatus was found by Dan Engstrom, John Satterlee and myself in an area also to be inundated by the Kickapoo Dam. Morrison (pers. comm.) considers this snail probably endangered and certainly a candidate for the list of species that are likely to become endangered.

The total known range of *Discus macclintocki* "is an area about 10 feet long and a foot wide at the mouth of a cave in Bixby State Park, Clayton County, Iowa" in the Driftless Area (Hubricht, 1972, *Sterkiana*, 45: 33). The Duluth, Minnesota Chapter of the Izaak Walton League of America has prepared a resolution (J. G. Eaton, pers. comm., 1972) which includes a statement that "the present program of producing wetlands with a few exceptions is more environmentally sound by the plugging of ditches for areas that were once wetlands than by the impoundment of creeks in areas that are naturally dry." *Discus macclintocki* was used as an example; if it were thus flooded, it would probably become extinct. Just such a pending disaster has been uncovered recently by the Sierra Club in California (Roth, 1972, *Sierra Club Bull.*, June, p 6), where the habitat of an endangered snail is threatened by "the management of marshland for the benefit of waterfowl."

There are undoubtedly many other relict species in the Driftless Area, some of which are as yet undescribed.

The Driftless Area is perhaps a priceless preview of the future. This is what a far vaster area is predicted to be like prior to the next glacial period. The Driftless Area must be protected not only for its beauty (it is close in proximity, as a primitive undeveloped area, to major population centers) but also as a possible "seed" area for post glacial redistribution of species. There is, in summary, a strong case for a Driftless national, state and/or local park system which would include portions of Minnesota, Wisconsin, Iowa and Illinois.

* * *

ROLE OF LYMNAEID SNAILS AS FIRST INTERMEDIATE HOSTS FOR *PLAGIORCHIS NOBLEI* PARK 1936

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Abstract

Stagnicola reflexa (Say) and *Lymnaea stagnalis* (Say) serve as 1st intermediate hosts for *Plagiorchis noblei* Park 1936. Following ingestion of embryonated eggs of this avian trematode by these gastropods, sporocysts and cercarial generations develop. Data from experimental studies conducted at Iowa Lakeside Laboratory during the summers of 1968-69 indicate that laboratory-reared *S. reflexa* first become infected at room temperatures (72-76°F) when exposed to eggs 84 hours following extrusion from adult worms. Furthermore, experimental infections could still be established in snails 43 days after plagiorchiid eggs had been shed. Cercariae penetrate and encyst in a variety of aquatic 2nd intermediate hosts, usually insects. Definitive hosts (various birds and mammals) acquire their infections by ingestion of infected 2nd intermediate hosts.

Macy (1960, *J. Parasitol.*, 46: 337-345) established that light was the primary factor controlling cercarial emergence of a bat fluke, *Plagiorchis vespertilionis* (Müller 1784), Braun 1900. He reported that maximum numbers of cercariae emerged from *Lymnaea stagnalis* between 2100 and 0100 hrs. Experiments conducted during this present study indicate that cercariae of *P. noblei* also exhibit nocturnal periodicity. Seventy-two% of the cercariae emerged between 2030 and 0530 hrs. However, if infected snails were exposed to several days of continuous light, a large accumulation of cercariae were tolerated by the host.

Lang (1972, pers. comm.) observed that more than 45% of the snail's biomass can be comprised of larval plagiorchiids during peak infections. The maximum number of cercariae which emerged from a

single snail during a continuous 24 hour period was over 19,000; minimum number of cercariae from the same snail during the same length of time was approximately 12,000.

The duration of *Plagiorchis noblei* infections in their gastropod hosts was even more remarkable. In the laboratory, snails could harbor these infections for at least 10 months. During this time, more than 4 million cercariae were produced.

Data obtained during this study confirm the work of Daniell (1964, M.S. Thesis, Iowa State Univ. Sci. & Tech., Ames, Iowa, 84 p) and Williams (1964, *Diss. Abstr.*, 24: 4885) concerning low incidences of natural infections of *Plagiorchis noblei* in lymnaeid snails. During the summer and fall of 1969, a total of 4,361 snails representing 2 species of lymnaeids were collected in nature, individually isolated in the laboratory and examined for cercarial infections. Twenty-two of 2,691 (0.83%) *Stagnicola reflexa* and 19 of 1,670 (1.13%) *Lymnaea stagnalis* harbored natural infections of *P. noblei*. Natural infections from both species of snails over the entire summer averaged 0.91%. These data indicate that in nature lymnaeid populations are not adversely affected by *P. noblei* infections.

Lack of host specificity and the wide distribution of its hosts, especially snails, are responsible for the cosmopolitan distribution of *Plagiorchis noblei*. In nature, the close proximity of various aquatic gastropods known to harbor plagiorchiids, as well as the presence of a diversified group of animals serving as 2nd intermediate and definitive hosts, facilitates the occurrence of these worms in a variety of hosts.

In summary, these 2 species of lymnaeids, and perhaps others, are ideally suited as 1st intermediate hosts of *Plagiorchis noblei* for the following reasons: (1) an individual snail can harbor large numbers of cercariae, (2) gastropod hosts are widely distributed, (3) low incidence of natural infections does not adversely affect lymnaeid populations, and (4) snails can withstand infections for at least 10 months.

* * *

TRANSMISSION OF OSTRACODS IN SNAILS[1]

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Abstract

Observations were made, perhaps for the first time, that ostracod eggs can be harbored and passed in a viable state through the intestines of snails in culture. Altogether, 65 ostracod eggs were found in the feces from 13 of 20 *Biomphalaria tenagophila* snails taken from an aquarium infested with *Cypricercus reticulatus* ostracods. Some 10 of the 65 ostracod eggs hatched within 6 days after they were discharged in snail feces at a temperature of 24°C to 27°C. When 20 other ostracod-infested *B. tenagophila* were dissected and their digestive tracts examined, altogether 19 ostracod eggs were found. Of these, 12 came from the crop-gizzard-pylorus portion. Other data further indicated that ostracod eggs can be retained in this portion for a considerable period of time.

Both *Biomphalaria tenagophila* and *B. pfeifferi* were fed ostracod eggs. Intact ostracod eggs were later recovered from the feces of both species. Snails were able to ingest more than one ostracod egg at a time, which were discharged intermittently for a 6-24 hour period. Of *B. pfeifferi*, 3 of 4 discharged ostracod eggs hatched within 3 days after being deposited in water at temperatures maintained between 28°C to 30°C. One newborn ostracod matured and reproduced parthenogenetically at the age of 13 to 14 days at the same temperature range. This animal produced an average of 21.2 eggs per day with a total of 297 eggs in 14 days and had an 83.8% viability.

[1]This work was carried out under the sponsorship of the Commission on Parasitic Diseases, Armed Forces Epidemiological Board and was supported by the Office of the Surgeon General, Department of the Army.

* * *

INCIDENCE OF A PARASITIC LEECH *MARVINMEYERIA* [=*OCULOBDELLA*] *LUCIDA* MOORE AND TWO CERCARIAL TYPES IN ESTIVATING *STAGNICOLA EXILIS* (LEA)[1]

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Abstract

Leeches in the family Glossiphoniidae include the so-called snail-leeches. However, very little data are available as to which snails are parasitized or eaten by which species of leeches, or which other para-

[1]This investigation was supported, in part, by PHS Training Grant No. 5 T1 AI 41 from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service.

sites infect snails infested by particular species of leeches.

Past studies on leech-snail relationships have been of 2 general types, survey and experimental. The survey type of investigation is found in the works of the following investigators: Jacquet, 1885, *L'Exchange* No. 1: 2; Castle, 1900, *Bull. Harvard Mus. comp. Zool.*, 36: 17-64; Moore, J. P., 1901, *Bull. Ill. State Lab. natur. Hist.*, 5: 479-547; Moore, J. P., 1924, *Univ. Toronto Stud.*, Biol. Ser., 23: 17-31; Moore, J. P., 1939, *Puerto Rico J. publ. Hlth. trop. Med.*, 14: 422-429; Nachtrieb, Hemingway, & Moore, J. P., 1912, *Geol. natur. Hist. Surv. Minn.*, Zool. Ser., 5: 1-150; Elliot, 1917, *Proc. malacol. Soc. London*, 12: 307; Miller, 1929, *Contr. Franz T. Stone Lab., Ohio State Univ.*, 2: 1-38; Miller, 1937, *Ohio J. Sci.*, 37: 85-90; Krull, 1931, *Occ. Paps. Mus. Zool., Univ. Mich.*, No. 226: 5; Guibe, 1936, *Soc. Linn. Norvandie Bull.*, 8 Ser., 8: 73-79; Pawlowski, 1936, *Arch. Hydrobiol. Rybact.*, 10: 1-47; Volz & Frömming, 1936, *Arch. Molluskenk.*, 68: 211-213; Herter, 1937, *In:* Bronns, *Klassen und Ordnungen des Tierreichs*, 4, (3), 4: 321-496; Autrum, 1939, Literatur über Hirudineen, *In:* Bronns, *Klassen und Ordnungen des Tierreichs*, 4, (3), 4, Hirudineen; Boisin-Bennike, 1943, *Fol. Limnol. Scand.*, 2: 1-109; Mathers, 1948, *Iowa Acad. Sci.*, 55: 397-424; Mann, 1955, *J. Animal Ecol.*, 24(1): 98-119; Mann, 1962, *Leeches (Hirudinea), their Structure, Physiology, Ecology, & Embryology.* Pergamon Press, New York, p 139-144; Michelson, 1957, *J. Parasitol.*, 47: 416; Malek, 1958, *Bull. Wld. Hlth Org.*, 18: 809-810; Moore, J. E., 1964, *Natn. Mus. Can. natur. Hist. Paps.*, 27: 1-15; Soós, 1964, *Opusc. Zool.* (Budapest), 5(1): 107-112; Gruffydd, 1965, *Ann. Mag. natur. Hist.*, 13(8): 151-154; Sapkarev, 1967, *Trans. Wis. Acad. Sci.*, 56: 225-253; Hatto, 1968, *Hydrobiologia*, 31: 363-384; Sawyer, 1968, *Ohio J. Sci.*, 64(4): 226-230; Sawyer, 1972, *Ill. Biol. Monog.*, 46: 1-154; Sarah, 1971, *Ohio J. Sci.*, 71(1): 15-20; and Klemm, 1972, *Mich. Academician*, 4(4): 405-444. These authors have indicated that certain leeches are enemies of snails under natural conditions or in aquaria, and that the leech-snail relationships may be the host-parasite type or the prey-predator type.

The experimental type of investigations are found in works of Brumpt, 1941, *Ann. Parasitol.*, 18: 9-45; Waffle, 1963, M.S. Thesis, Univ. of Iowa, Iowa City; Cernin, Michelson & Augustine, 1956, *Amer. J. trop. Med. Hyg.*, 5: 308-314; MacAnnally & Moore, D. V., 1965, *J. Parasitol.*, 51(2): 32; and MacAnnally & Moore, D. V., 1966, *J. Parasitol.*, 52(1): 196-197. These authors have shown that certain leeches will attack certain snails by sucking the blood or eating the soft parts of the animal when both were confined in the same aquarium. These studies have been interpreted as a prey-predator relationship.

My current research is directed at determining the ecological relationships between snails and leeches in the Huron River drainage system of Michigan, U.S.A. From this study, hopefully, the effectiveness of leeches as regulators of snail populations can be ascertained. The study includes the examination of many species of snails for leeches at specific locations from different habitats such as creeks, rivers, lakes, ponds and woods pools.

Past collecting from woods pools during spring and summer showed that *Stagnicola exilis* (Lea), *S. palustris* (Say), *Aplexa hypnorum* (Linnaeus), *Helisoma trivolvis* (Say), *Planorbula armigera* (Say), *Menetus exacuous* (Say) and *Gyraulus parvus* (Say) were infested with leeches. But in early August, depending on the amount of precipiation, many woods pools dry up. Snails found there, consequently, either die or must estivate by burrowing into the bottom mud and debris or by secreting an epiphragm. Leeches, moreover, either die or are assumed to burrow in the substratum for survival.

In the course of my collecting, an interesting observation was made on the estivation of a colony of *Stagnicola exilis*, which were found attached to tree trunks, fallen branches, rooted plants, etc. This estivating condition was reported by Sterki (1912, *Nautilus*, 26(6): 64-65) and van der Schalie (1940, *Nautilus*, 53(4): 134-135). According to the latter, this behavior is quite different from that of the many other species of aquatic pulmonates that usually inhabit temporary woods pools. Therefore, a preliminary study was conducted during the dry period in a woods pool in Washtenaw County, Michigan to determine if leeches or trematode larvae occurred inside the estivating *S. exilis*. The woods pool had been dry for 3 weeks; the shells of the *S. exilis* varied in length from 18 mm to 25 mm. The frequency of occurrence of immature *Marvinmeyeria lucida* and 2 cercarial types that were found inside of *S. exilis* is presented below. This is the first report of a leech infesting an estivating snail.

Percent frequency of occurrence of *M. lucida* and 2 types of cercariae on 100 *S. exilis*.
M. lucida: 41/100=41% Echinostome: 9/100=9% Amphistome: 7/100=7%

These data on the percent frequency of occurrence indicate that out of 100 specimens of *Stagnicola exilis* collected, 41% were infested with the leech *Marvinmeyeria lucida*, 9% were infected with echinostome larvae and 7% were infected with amphistome larvae. This gave a total frequency of 57% occurrence of both the leech and trematode larvae. Of the specimens of *S. exilis* infested with leeches, 34 (90%) of the snails were infested with 1 leech, 3 (7%) were infested with 2 leeches and 1 (2%) was infested with 3 leeches. Of the 46 leeches found on the snails, 41 (89%) were found above the mantle (between the shell and mantle in the vicinity of the albumen and digestive glands). Three (7%) of the 46 leeches were taken from the mantle cavity, and 2 (4%) were found inside the kidney. No leeches were found on those snails that had a trematode infection, and in the latter no snails were found with multiple cercarial types.

The gut contents of *Marvinmeyeria lucida* were tested by an immunological technique for the presence of molluscan tissue. This was done by observing the reactions of the gut contents of *M. lucida* against prepared molluscan antisera. The procedures used were a modified micro-Ouchterlony agar gel diffusion method (see Davies, 1969, *Oikos*, 20: 248-260; Burch & Lindsay, 1970, *Malacol. Rev.*, 3: 1-18). The presence of precipitin arcs demonstrated that *M. lucida* had been parasitizing the snails.

* * *

Biologists attending the Mollusk Seminar, Ann Arbor, Michigan, U.S.A., 25-26 August 1972. Left to right: E. H. Michelson, J. B. Burch, G. A. Te, Patricia A. Ayers, David H. Stansbery, W. H. Heard, C. S. Richards, E. A. Malek, Amy L. Shrader, C. J. Bayne, Virginia Vale, P. T. LoVerde, George M. Davis, C. M. Patterson, R. S. Houbrick, Carol B. Stein, Donald J. Klemm, Jean M. Gaillard, Harvey D. Blankespoor, S. K. Wu, Robert Robertson, F. M. A. Ukoli, J. E. Baxter, Paul H. Rudolph, Janet W. Rudolph, Albert J. Burkey, Irene Lubinsky, Mrs. A. J. Burkey, Esther M. Goudsmit, B. J. Kidd, G. K. Lindsay, Henry van der Schalie, Y. S. Liang, E. H. Atkinson, J. W. Atkinson, N. H. Verdonk, James N. Cather. Not pictured: Elmer G. Berry, Arthur H. Clarke, Marc Imlay, *Louise R. Kraemer*, Sharon C. McDonald, Gary L. Pace, Alex Tompa.

MISCELLANEA

MALACOLOGIA - TEN YEARS OF PUBLICATION

MALACOLOGIA has now completed 10 years of publication, and as soon as the volumes currently in press are distributed, the journal will have published 13 volumes. Vol. 1, No. 1 appeared in late 1962. Initiating and producing the journal has been an experiment in economical publication of high quality scientific papers, directed and edited by a small editorial and managerial staff, but substantially assisted by a large international editorial board. It has also been a highly successful experiment in cooperation among scientists from many nations. A brief recapping of the early history of the journal, as well as a current status report, follows. For an earlier report on the first 5 years of publication, see Burch & Huber (1967, *Amer. malacol. Union, ann. Reps.*, Bull. 34, p 29-30).

Several malacologists (J. B. Burch, Melbourne R. Carriker, Robert Robertson and Dwight W. Taylor) attending the annual meeting of the American Malacological Union in June, 1961, discussed the feasibility of promoting an international journal which could publish either short or long papers on any aspect of malacology and in one of several different languages. A need for such a journal had already been recognized for quite some time in the United States, especially by those active at the major malacological research institutions. For that reason, J. B. Burch had decided as early as 1959 to look into economical and practical means of producing such a journal, and in the following year came to the conclusion that it was indeed possible to initiate a periodical of reasonable standards on a practical basis at an economical cost. This conclusion was the impetus for the initial meeting of interested colleagues at the 1961 A.M.U. meetings.

Early in 1962 Elmer G. Berry, Allyn G. Smith and Norman F. Sohl became affiliated with those malacologists interested in a new journal, and later they were joined by J Frances Allen, Kenneth J. Boss, George M. Davis and Charles R. Stasek. This group, which sponsors and directs *MALACOLOGIA*, was incorporated under the laws of the state of Michigan as the Institute of Malacology in December, 1961. Norman F. Sohl of the U.S. Geological Survey is currently President of the Institute of Malacology. Past Presidents are Melbourne R. Carriker of the Marine Biological Laboratory, Woods Hole, Dwight W. Taylor of the U.S. Geological Survey, Elmer G. Berry of The University of Michigan, and Allyn G. Smith of the California Academy of Science. Robert Robertson of the Academy of Natural Sciences of Philadelphia is currently the President-Elect.

Although the need for a new malacological journal to help meet the increasing demands of mushrooming research was felt by us, we were not convinced that our colleagues throughout the world felt the same way. Accordingly, a questionnaire was submitted in 1961 to 192 malacologists and other zoologists working with mollusks. The group to which it was sent did not represent the entire malacological community, but it was broadly representative of malacology all over the world. The group consisted of members of various zoological societies, of scientists who were carrying on research, who actively published and who were associated with institutions granting advanced degrees. The response was encouraging: 80% of the questionnaires were returned; 92% of those who replied favored establishment of a new journal as proposed, and many favored it strongly; 6% were undecided and only 2% opposed the establishment of such a journal.

The funds for the establishment of *MALACOLOGIA* and for its maintenance during the production of the first 3 volumes were generously awarded by the U.S. National Science Foundation (a grant of US$ 11,037). The initial direction of the journal was by J. B. Burch as Managing Editor and Anne Gismann as General

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Editor. In 1966 Dr. Burch was named Associate Editor after he was succeeded as Managing Editor by J. M. Huber. Miss Huber was succeeded by C. M. Patterson; S.-K. Wu is the current Managing Editor. In 1969, Dr. Burch joined Mrs. Gismann as a General Editor, to be succeeded in that post by C.J. Bayne when he (Burch) became Editor-in-Chief in 1970.

MALACOLOGIA has tried to have a competent and truly international editorial board. The editorial board currently consists of 60 editors who represent the following 27 countries: Australia, Austria, Brazil, Canada, Chile, Denmark, Egypt, Ethiopia, Finland, France, Germany (DR), Germany (FR), Hungary, India, Italy, Japan, Netherlands, New Zealand, Norway, Rumania, South Africa, Sweden, Switzerland, Uruguay, U.K., U.S.A. and U.S.S.R.

Authors contributing papers to the first 13 volumes of *MALACOLOGIA* represent the following countries: Argentina, Australia, Austria, Brazil, Canada, Denmark, Egypt, France, Germany (FR), Hong Kong, Hungary, India, Italy, Japan, Liberia, Netherlands, New Zealand, Nigeria, Norway, Portugal, Rhodesia, Rumania, South Africa, Spain, Sweden, Switzerland, Thailand, Taiwan, U.K., U.S.A., U.S.S.R., Venezuela and Yugoslavia.

Through Vol. 11, *MALACOLOGIA* has published 276 articles by 245 different authors. The shortest paper contained 3 pages[1], the longest 434 pages. The average length of the papers in Vols. 1-5 was 25 pages; for Vols. 6-11 the average length of each paper was 24 pages[1]. Areas of research dealt with in articles published to date include anaesthetization, behavior, biochemistry, communal relationships, comparative and descriptive morphology, conchology, conchometry, cytogenetics, cytotaxonomy, development, ecology, evolution, functional morphology, genetics, growth, histochemistry, natural history, paleontology, parasitism, phylogeny, physiology, predation, radiation biology, regeneration, symbiosis, systematics, techniques, variation, zoogeography and distribution, and zoological nomenclature.

The various articles in *MALACOLOGIA* have been published in their original languages, which in the first 13 volumes included English, French, German, Russian and Spanish. The great majority of the papers have been in English. In the first 4 numbers of *MALACOLOGIA*, abstracts of each article were printed in 5 languages: English, French, German, Russian and Spanish. However, providing this service caused undue difficulties and expense, and resulted in considerable delay of publication of each issue. Accordingly, beginning with Vol. 2, No. 2, and until Vol. 7, when French resumed, *MALACOLOGIA* restricted the preparation of abstracts to one Germanic language (English), one Romance language (Spanish) and one Slavic language (Russian), unless other abstracts were supplied by the authors. German abstracts resumed with Vol. 11. We were able to continue the French and German abstracts through the good services of Albert Lucas, Claus Meier-Brook and Hildegard Zeissler. Abstracts are translated into Spanish by J. J. Parodiz and into Russian by Z. Filatova.

Abstracts of *MALACOLOGIA* articles are published by *Biological Abstracts*, the Institute of Scientific Information of the U.S.S.R. Academy of Sciences and The Food and Agricultural Organization of the United Nations.

MALACOLOGIA will publish the abstracts and/or the full articles of the Fourth European Malacological Congress, held in Geneva, in September, 1971. These will go into a special Proceedings issue, similar to that published for the

[1]Excluding the 1 and 2 page abstracts of the European Malacological Congresses and the contributions to the American Malacological Union's Symposium on Rare and Endangered Mollusks (Vol. 10, No. 1).

Second and Third Congresses. *MALACOLOGIA* also published the Proceedings of the First European Malacological Congress, not as an issue of the journal, but as a separate publication for the Congress Committee.

The photo-offset copy for the printing of *MALACOLOGIA* is prepared in the Museum of Zoology, The University of Michigan, with a Friden Justowriter recorder and reproducer and 3 I.B.M. typewriters. The funds ($7900) for the purchase of this typing equipment came from subscription payments for the journal.

Because of the high printing costs in the United States, 2 issues (Vol. 9, No. 2 and Vol. 10, No. 2) have been printed in India, and another (Vol. 13, No. 1-2) is currently in press there. However, because of communication difficulties and slowness in printing, future issues will not be published in India (although slowness is not confined to India; we have had similar problems with printers in the U.S.A.). Vol. 12 is currently being set in type and printed by the Printing Office of The University of Michigan.

Costs for supporting personnel to prepare photo-offset copy in the Museum of Zoology, as well as for many subsidiary production costs, have been provided by The University of Michigan through the courtesy of the Editor-in-Chief. In this way, production of the journal has been substantially subsidized by the University.

Two main problems have been with the journal since its inception: 1) publishing in a reasonably short time the many, often large, manuscripts accepted by the Editorial Board; and 2) the steadily increasing inflation in the United States and the resulting increase in publication costs. Because the editorial staff is small, and editing and management of the journal has to be done by them as a job additional to their other professional duties, editing has sometimes been slow. However, in spite of this, the publication of 13 volumes in 10 years is a significant accomplishment. Although submitted manuscripts are rigorously reviewed by at least 2 members of the Editorial Board, and only those papers judged to meet a high standard are accepted for publication, the journal has continually accepted more papers than it can publish at the rate of one volume per year. Perhaps a solution to the continued backlog of manuscripts (which increases the time between the acceptance of the papers and their publication) might be to raise the standards for acceptance of manuscripts even higher, or to set a limit on the size of manuscripts to be accepted, or to simply not accept papers during periods of accumulated unpublished manuscripts.

Continued increase in publication costs because of inflation is a problem perhaps more difficult to deal with than that of an excessive number of manuscripts. More inexpensive methods of printing might be used to keep costs minimal, although without a new break-through in printing technology, cheaper printing would usually mean a decrease in quality and appearance of the journal. Or the journal might be printed in another country, where costs are relatively less.

Information on subscriptions for the first 5 years can be summarized as follows (total for each year): 223 subscriptions for 1962, 525 for 1963, 651 for 1964, 698 for 1965 and 715 for 1966. As of early 1972, the number of paid subscribers was about the same as in 1966, i.e., for the past several years the journal has been adding new subscribers at about the same rate as old subscribers failed to renew. Three hundred and sixty-five of the current subscriptions are from the U.S.A. and 340 from other countries. Numbers of subscriptions by country are as follows: Algeria (1), Argentina (6), Australia (14), Austria (4), Belgium (5), Brazil (15), Bulgaria (1), Canada (40), Chile (3), Colombia (1), Cyprus (1), Denmark (4), Egypt (3), Ethiopia (1), Finland (2), France (22), Germany, DR (1), Germany, FR (26), Ghana (1), India (7), Iraq (2), Israel (2), Italy (8), Japan (28), Korea (2), Lebanon (1), Malaysia (2), Malagasy (2), Mexico

(3), Monaco (1), Mozambique (1), Netherlands (17), New Zealand (9), Nigeria (1), Norway (4), Philippines (2), Portugal (2), Rhodesia (1), Senegal (1), Singapore (1), South Africa (10), Spain (3), Sweden (8), Switzerland (5), Taiwan (3), Thailand (2), Uruguay (1), U.K. (47), U.S.A. (365), U.S.S.R. (6), West Indies (2) and Yugoslavia (5). A summary of private vs. institutional subscriptions is as follows: U.S.A., 112 private subscriptions vs. 253 institutional subscriptions; non-U.S.A., 92 private subscriptions vs. 248 institutional subscriptions. That is, over 2/3 of both the United States and foreign subscriptions are institutional.

Subscription price for *MALACOLOGIA* was originally US$ 5.00 per volume in 1962. Since then it has been necessary to raise the subscription price several times because of continued inflation in the U.S.A., where most issues of the journal are printed. It is currently US$ 9.00 per volume for private subscribers, US$ 15.00 for North American Institutions, and US$ 12.00 for all other institutions. An extra charge (US$ 1.00 per volume) is added for subscriptions handled by North American subscription agencies (to help offset the added handling expense).

In 1972 the business office of *MALACOLOGIA* was transferred from Ann Arbor to Philadelphia (Academy of Natural Sciences). In 1973 the editorship will also be transferred there.

J. B. BURCH, Editor-in-Chief

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ANNOUNCEMENTS AND NEWS

* * *

COUNCIL OF SYSTEMATIC MALACOLOGISTS. — On November 16th and 17th, 1972, malacologists representing many of the major molluscan collections in North America met in Philadelphia, Pennsylvania, U.S.A. As a result of this meeting, it was decided to form a "Council of Systematic Malacologists." At present this is a group without membership rolls, dues, constitution or bylaws, but its members share an interest in and concern for both malacology as a science and the systematic resources that are basic to molluscan research. Membership is open to all professional persons in the Americas who use or manage systematic malacological resources. Periodic meetings will be held in adjunct with scheduled scientific meetings or as needed to confer on common problems. The next meeting is scheduled for early April, 1973, in Chicago. Those wishing further information should contact Dr. Alan Solem, Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.

Malacologists meeting in Philadelphia, Pennsylvania, U.S.A. on November 16th and 17th, 1972, to form the "Council of Systematic Malacologists." Left to right, front row: Robert Robertson, George E. Radwin, R. Tucker Abbott, Kenneth J. Boss, James H. McLean, Middle row: Joseph Rosewater, George M. Davis, J. B. Burch, Alan Solem. Back row: David H. Stansbery, Arthur H. Clarke, Hal Lewis, Virginia Orr Maes.

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ARMY CORPS OF ENGINEERS GIVEN GO-AHEAD TO START TENNESSEE-TOMBIGBEE BARGE CANAL. — The Tombigbee River of northeastern Mississippi is one of the few relatively untouched rivers in the southeastern United States, an area once famous for its many scenic rivers with their rich, varied and highly endemic faunas. On August 4, 1972, federal judge William C. Keady handed down a decision in Aberdeen, Mississippi, that will allow the Army Corps of Engineers to proceed with its mammoth 10-year project to make a barge canal out of much of the Tombigbee River and to join the river with another major drainage basin, the Tennessee Valley. This river-turned-barge canal will provide a short-cut for barges, allowing them to reach the Gulf via Mobile, Alabama, rather than New Orleans, Louisiana. The length of the project is 253 miles, traversing a drop in elevation of 341 feet from where the canal will join the Tennessee River. The bottom width of the canal is to be 280-300 feet, and, especially in the upper reaches, it will require a great displacement of earth (one of the scientists testifying at the trial calculated that if the dirt dug up were piled 100 feet by 100 feet wide, it would extend for 40 miles; the Army had no clear conception of what it would do with the dirt, even though it conceded that such an amount of dirt dumped on the surrounding landscape would have an adverse environmental effect).

Eleven biologists from diverse fields testified as to the expected environmental damage and what they considered were serious deficiencies in the Army's Environmental Impact Statement (a statement required by the National Environmental Policy Act) in describing the damage that would likely be caused by the project. Malacologists questioned the adequacy of the impact statement on the grounds that it hardly mentioned mollusks and that the several statements that could be related directly to mollusks were so brief as to be useless, irrelevant or erroneous. (For example, although well over 150 species of gastropods have been described from the Tombigbee-Alabama-Mobile river system, with over 70% endemism within the system, and a similar number of species and amount of endemism is found in the Tennessee River system to the north (with only 12% of the species being common to both systems), no reference could be found in the impact statement that freshwater snails exist in any of the rivers of the two systems.) Nearly all biologists testifying in behalf of the Environmental Defense Fund (including malacologists) took exception with the statement, "No known rare or endangered species [of animals] exist within the project area."

Malacologists expressed the concern that the projected canalization of the river would destroy the mollusks and their habitats and that joining the two drainage systems would result in the extinction of many species in one of the richest and most highly endemic areas for freshwater mollusks in the world. Because so little is yet known about most of these species, malacology would suffer irreparable damage. Many of the surrounding rivers have already suffered greatly by man's onslaught of riverine ecosystems, and some are now nearly devoid of mollusks. Biologists testifying in behalf of the Environmental Defense Fund were Dr. Lincoln P. Brower (Amherst College), Dr. J. B. Burch (University of Michigan), Dr. Richard Dale Caldwell (Texas A. & M. University), Mr. John E. Cooper (Baltimore Community College), Dr. George Folkerts (Auburn University), Dr. Clarke Hubbs (University of Texas), Dr. Gerome Jackson (Mississippi State University), Mr. Richard Marshall (Mississippi State University), Dr. Carl Monk (University of Georgia), Dr. David H. Stansbery (Ohio State University) and Dr. James E. Williams (Mississippi State College for Women; present institution - Tuskegee Institute). Other prominent biologists sympathetic to the Environmental Defense Fund's suit against the Army Corps of Engineers were present at the trial as observers.

In regard to mollusks, testimony in support of the Army Corps of Engineers indicated that loss of various mussel and snail species in this riverine ecosystem would not be significant from an ecological point of view because other organisms can perform their roles. Three biologists testified for the Corps of Engineers: Dr. Daniel J. Nelson (Oak Ridge National Laboratory), Mr. John M. Bates (Ann Arbor, Michigan) and Dr. Ralph H. Chermock (Parsons College). The 2 Army Corps of Engineers' biologists responsible for the biological sections of the Corps' Environmental Statement, Mr. Hugh McClellan and Mr. Jack Mallory, were not placed on the witness stand by the Corps of Engineers' lawyers.

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SOCIETIES' NEWS

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FIFTH LATIN AMERICAN CONGRESS OF ZOOLOGY. — The Fifth Latin American Congress of Zoology was held in Montevideo, Uruguay, 18-23 October 1971. One of the sponsors of the Congress was the Sociedad Malacológica del Uruguay, whose President, Dr. Miguel A. Klappenbach, was also President of the Congress Committee. Malacologists serving on the National Commission hosting the Congress were Eliseo Duarte, Violeta B. de Langguth, Susana Maytía de Scarabino, José Olazarri, Victor Scarabino and Elías H. Ureta. Papers presented on mollusks at the Congress are listed below.

Una nueva forma de ciliado Thigmotrichidae de la cavidad paleal de *Mactra isabelleana* (Mollusca Lamellibr.). E. Dei-Cas & F. Mañé-Garzón.

Ecologia de una poblacion de berberecho, *Donax hanleyanus* Phil., en villa Gesell (Provincia de Buenos Aires, Argentina). Pablo E. Penchaszadeh & Santiago Raúl Olivier

Scaphopoda (Moll.) del sur del Brasil, Uruguay y Provincia de Buenos Aires. (Sistematica - distribucion) Víctor Scarabino

Lista de los ejemplares - tipo depositados en el Museo Nacional de Historia Natural de Montevideo, Uruguay. II. Mollusca. José Olazarri, Alvaro Mones & Eliseo Duarte

La familia Thraciidae (Moll. Pelecypoda) en el area Atlantica de America del Sur. Miguel A. Klappenbach & E. H. Ureta

Notas sobre Strophocheilidae. V. Posible origen y distribucion de las especies Uruguayas. Miguel A. Klappenbach & José Olazarri

Aplicacion de algunos parametros biometricos en la estimacion de la biomasa de gasteropodos dulceacuicolas. Danilo H. Di Persia

Algunos aspectos de la biologia y ecologia de la vieira (*Chlamys tehuelcha* D'orb) del Golfo San Matias (Pcia. de Rio Negro, Argentina). Santiago Raúl Olivier, Haraldo E. Chistiansen & Ruben Marziale

El genero *Scalarinella* Dohrn, 1874 (Moll. Gastropoda) en el Uruguay. Miguel A. Klappenbach & José Olazarri

Notas sobre Strophocheilidae. VI. Contribucion al conocimiento de *Austroborus cordillerae* (Doering, 1876). Miguel A. Klappenbach & José Olazarri

Estructura de la comunidad de playa arenosa de Casino (Rio Grande do Sul, Brasil). Pablo E. Penchaszadeh

Estructura trofica de la comunidad de *Mytilus platensis* de bancos situados al NE de Mar del Plata, Argentina). Pablo E. Penchaszadeh

Sobre *Helix elevata* Orbigny, 1835 (no Say, 1821) *Helix paraguayana* Pfeiffer, 1842 (Moll. Gastr.) Miguel A. Klappenbach & José Olazarri

Contribuicao ao estudo morfo-anatomico de *Leila blainvilleana* (Lea). Inga Ludmila Veitenheimer

Morfologia do sistema digestivo de *Castalia undosa martensi* (Ihering, 1893) (Bivalvia: Hyriidae). María Cristina Dreher Mansur

Los generos *Crassatella* Lamarck 1799 y *Crassinella* Guppy 1874 en el Atlantico Sudamericano. Miguel A. Klappenbach & Victor Scarabino

Moluscos de la expedicion del "Walter Herwig" al Atlantico Sudoccidental (1966) depositados en el Instituto de Biologia Marina de Mar del Plata (excepto cefalopodos). Santiago Raúl Olivier & Victor Scarabino

Sobre a distribuicao biogeografica de moluscos comestiveis no litoral do Brasil. Hans Jakobi

Moluscos comerciales del Peru. Gregorio Mario Peña Gonzáles

Una tecnica simple para la anestesia, fijacion y preservacion extendida de *Aplysia* sp. (Opisthobranchia, Mollusca) con destino a materiales de museo y enseñanza. A. Spiritoso

Um novo *Phyllocaulis* do Brasil (Veronicellidae, Gastropoda). José Willibaldo Thomé.

NATIONAL SHELLFISHERIES ASSOCIATION. — The 64th annual meeting of the Shellfish Institute of North America and the National Shellfisheries Association was held in Williamsburg, Virgina, U.S.A., 25-29 June 1972. The business meeting was held on 29 June 1972. A brief resume of the meeting follows. *Financial report:* The Association is solvent, but many still owe dues. Eight states and one industry member continue as sustaining members. The *Site Committee* reported the 1973 meeting would be in New Orleans the 3rd week in June and the 1974 meeting would be held in Philadelphia. *Dues:* Annual dues will be US$ 8 effective January 1973. *Constitutional amendment:* Artical 4, Section A was amended to include a president-elect and one vice-president instead of 2 vice-presidents. *New members:* 29 new members were accepted by the association. The *Thurlow Nelson Award* for the outstanding paper by a young biologist was awarded to Mr. Ed Cake for his paper on "Larval cestode infestations in several edible bivalve mollusks from the vicinity of St. Teresa, Florida." *Resolutions* were passed honoring Dr. Imai for his outstanding work in shellfish biology, and Mrs. Helen Haynie, retiring secretary-treasurer, for her NSA work over the past 6 years. *Election committee report:* The new officers are: President - R. Winston Menzel; President-elect - Ron Westley; Vice-president - Dexter Haven; Secretary-treasurer - Michael Castagna; Member at large - Herb Hidu.

Sally Otto has been appointed co-editor of the *Proceedings*. All 100 copies of Ed Joyce's "Oyster Bibliography," ordered by Ken Chew for the Association, sold out in less than a week. President Menzel has accepted a position for 1 academic year as Visiting Professor of Marine Biology at Texas A & M University. His address is Department of Biology, Texas A&M University, College Station, Texas 77843, U.S.A.

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE. — The French Society of Malacology is an association governed by the French law of 1901. It is controlled by an Administrative Council of 12 members, elected for 3 years by the General Assembly. A 3rd part of the Council is renewable each year, the leaving members being re-eligible. The main body of the Council, elected for a period of one year of office, is composed of a President, a Vice-President, a General Secretary, a Deputy Secretary and a Treasurer. The Council is obliged to meet once every three months. Each year it invites to its meetings some non-French members of the Society. On 1 January 1972, the Society had 215 members.

The French Society of Malacology was founded on 29 January 1969. Its object is to encourage and develop all studies concerning Recent and fossil molluscs, to facilitate communication between malacologists and to inform them about current research in the different laboratories in France and other countries. The Society organises congresses, sets up symposia and is in favour of working groups. The themes of recent symposia are: Ecology and Paleoecology of Molluscs (Caen, 1970), Sexuality in Molluscs (Caen, 1970), Alpine Molluscs (Lyon, 1971), Calcium in Molluscs (Besançon, May 1972), Applied Continental Malacology (Rouen, September 1972). "The Continental Fauna Commission," a working group functioning since 1970, is concerned with the inventory and geographic distribution of Recent molluscs in France.

Membership in the Society may be obtained by writing the Secretariat of the Society (55, rue Buffon, Paris 5e, France). No special conditions are necessary to become a member. The membership forms are examined at the time of each reunion of the Administrative Council. The yearly membership fee is 35 francs (students: 25 francs). This fee gives the right, apart from the journal *Haliotis*, to all the Society's publications. Membership fees and orders for publications are payable by international postal order made out to "Société Française de Malacologie, 55 rue Buffon, Paris 5e, France." Banker's cheques should be sent directly to the Treasurer of the Society.

The French Society of Malacology publishes the journal *Haliotis* (a yearly volume made up of one or more numbers). *Haliotis* publishes original articles and reviews. The communications of Congresses and the reports on symposia take priority for publication. The volumes of *Haliotis* are sold for 50 francs each. Contents of past volumes are as follows: Vol. 1, 1971, no. 1 - Congress at Caen; Vol. 1, no. 2 - Symposia at Caen (Sexuality; Paleoecology and Ecology); Vol. 2, 1972, no. 1 - Meeting at Lyon (Molluscs of the Alps); Vol. 2, no. 2 - Symposium at Besançon (Calcium in Molluscs); Vol. 3, 1973, no. 1 - Symposium at Rouen (Applied Continental Malacology). Individual numbers cannot be sold separately. Also available is the Yearbook of the Members of the Society.

The subscription to *Haliotis* is 50 francs a year for all Organisations (laboratories, museums, societies and libraries). The institute or organisation which subscribes to the journal is considered a legal member of the Society; they receive in addition to a copy of *Haliotis* all leaflets and circulars sent to members.

AN HISTORICAL OUTLINE OF MALACOLOGY IN ITALY. — The first Italian malacological periodical publication was started in 1868. In that year the 1st volume of the *Bullettino Malacologico Italiano*, directed by Giuseppe Meneghini and edited by Cammillo Gentiluomo, was issued in Pisa. Associated with the new journal were F. L. Appelius, A. Issel, E. Martens, V. Pecchioli, G. Stabile, P. Strobel, and A. and G. B. Villa. During the years to follow, many other well-known malacologists of the 19th century (e.g., G. Caramagna, C. D'Ancona, R. Lawley, A. Manzoni, C. Mella, A. Targioni Tozzetti, N. Tiberi, T. Allery di Monterosato, E. Bettoni, S. Brusina, G. Seguenza and H. C. Weinkauff) increased the number of associates. The *Bullettino Malacologico Italiano* appeared every 2 months for 7 years, until 1874 and Vol. 7. At the end of Vol. 7, an "Announcement" stated that the Italian Malacological Society was founded in Pisa: President, Guiseppe Meneghini; Vice-President, A. Targioni Tozzetti; Secretary, C. Gentiluomo; Vice-Secretary, C. De Stefani; and Treasurer, R. Lawley. This group started a new publication, the *Bullettino della Società Malacologica Italiana*. The 1st volume appeared in 1875 and the last one (Vol. 20) in 1899.

Unfortunately, near the end of the 19th century the number of founders and associates of the *Bullettino* and the members of the Società decreased, and the tradition of malacology, intensely carried out until then, rapidly faded. For the next 60 years there was very little malacological interest in Italy, while abroad in Germany, France and then in Great Britain the number of scholars and shell enthusiasts increased, leading to many important contributions to systematic and faunistic knowledge of European marine, freshwater and land Mollusca. In Italy the efforts of a few regional malacologists such as G. Lepri, R. Bellini, F. Settepassi, C. Allegretti, C. Piersanti, D. Graziadei and F. Schrott were not sufficient to carry on a great amount of research. However, particular mention should be made of the work by Carlo Alzona and Jole Bisacchi Alzona on the systematics and biogeography of the Continental Molluscan fauna.

In 1962, during the 1st European Malacological Congress, 3 Italian malacologists, C. F. Sacchi, F. Settepassi and F. Toffoletto, casually met in London. They discussed the formation of a malacological organization, and on 10 January 1963, with the cooperation of about 10 persons, the Italian Malacological Society was founded in Milan. From 1963 until 1971, due to the small number of members, the only officer of the Society was the Secretary, Dr. Ferdinando Toffoletto. In 1972, by a change in the constitution, duties and

responsibilities were more reasonably divided among an Executive Committee: President, F. Toffoletto; Vice-President, C. F. Sacchi; Secretary-Treasurer, A. Girod; Publication Chairman, F. Ghisotti; and Councillor, O. Ravera.

The publication of the Italian Malacological Society, entitled "Lavori," is actually collected reprints of the members. The 1st volume appeared in 1964. Volume 9 (1972) has just been issued. The latter contains 11 papers authored by G. Barbato, G. Barsotti, L. Baldori, G. Frilli, F. Giusti, F. Levi-Setti, M. Mazzini, G. Pinna and F. Toffoletto.

For further information or request for membership (annual fee: US$ 7.00), write the Secretary, Società Malacologica Italiana, c/o Museo Civico di Storia Naturale, Corso Venezia 55, 20121, Milano, Italy. — (Alberto Girod)

NETHERLANDS MALACOLOGICAL SOCIETY. — Dr. C.O. van Regteren Altena of the Rijksmuseum van Natuurlijke Historie, Leiden, Holland, will retire on 1 January 1973, having reached the age of retirement. On the occasion of his 65th birthday in December 1972, the Netherlands Malacological Society (Nederlandse Malacologische Vereniging) published *Basteria*, Vol. 36, Nos. 2-5, as a dedication volume to Dr. van Regteren Altena, the former President of the Society and Editor-in-Chief of *Basteria*. This "Festschrift" (168 p) contains 16 papers by 17 authors covering a variety of malacological subjects. Financing this project was far beyond the normal financial resources of the society, but contributions by members and generous grants obtained from various sources have enabled the Society to pay its way in this respect. It contains the following papers:

- A sketch of the life and work of Dr. van Regteren Altena with portrait, list of papers and of new taxa (in Dutch with a summary in English) by Tera van Benthem Jutting & Van Bruggen.
- Three papers on marine bivalves by Johanna Nijssen-Meyer, Louise de Rooij-Schuiling and Ruth Turner (all in English).
- Four papers on land snails by Backhuys, Forcart, Gittenberger and Zilch (1 in English, 3 in German).
- Three papers on fossil molluscs by Janssen & Van der Slik, Spaink and Van Urk (1 in Dutch, 2 in English).
- Two papers on marine gastropods by Coomans and Van der Spoel (both in English).
- Two papers on historical aspects by Tera van Benthem Jutting and Dance (one in Dutch with an English summary, the other in English).
- One paper on freshwater bivalves by Kuiper (in French with an English summary).

All authors belong to the large circle of colleagues, friends and ex-pupils of Dr. van Regteren Altena: among these Ruth Turner, Peter Dance, Lothar Forcart and Adolf Zilch represent his friends and colleagues abroad.

The following names in the above papers have been dedicated to Dr. van Regteren Altena: *Regterenia* De Rooij-Schuiling (Mesodesmatidae), *Xylopholas altenai* Turner (Pholadidae), *Milax altenai* Forcart (Milacidae), *Ensis altenensis* Van Urk (Solenidae), *Altenaeum nortoni* Spaink (Condylocardiidae) and *Altenaia* Zilch (Enidae). (A. C. van Bruggen)

MALACOLOGICAL SOCIETY OF AUSTRALIA. — After 8 years of being run from Sydney, the Council and headquarters of the Malacological Society of Australia has reverted back to Melbourne. The new address to which all correspondence should be sent in the future is: Malacological Society of Australia, P.O. Box L 1277, G.P.O., Melbourne, Victoria 3001, Australia. The new Council of the Society is: Mrs. J. H. Black - President; Mr. R. C. Robertson - Secretary-Treasurer; Mr. R. Burn - Editor of the *Journal of the Malacological Society of Australia;* Dr. B. J. Smith - Editor of the Newsletter; Miss B. J. Nielsen - Council Member; Mr. T. A. Darragh - Council Member; Mr. J. Berrie - Council Member; Mr. K. McDowell - Council Member.

The next issue of the *Journal of the Malacological Society of Australia*, Vol. 2, No. 4 (1973) will be published in late March 1973.

ITALIAN MALACOLOGICAL UNION. — The Italian Malacological Union has in preparation the reprinting by photolithography of some old out-of-date works on Mediterranean molluscs. The authors are Brusina, Caramagna, Deshayes, Pallary and Tiberi. The works selected for this initial reprinting are of general interest; more specialized publications may be reprinted in the future. For further information contact The Italian Malacological Union, via De Sanctis 73, Milan, Italy, or D. A. Franchini, 37, via Cremona, Mantova, Italy.

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MEETING NOTICES

* * *

ASSOCIAÇÃO BRASILEIRA DE MALACOLOGIA. — The 3rd meeting of the Associação Brasileira de Malacologia will be held at the National Museum of Natural History during the 1st part of July 1973 in Rio de Janeiro, GB, Brazil. For further information, write Dr. Maury Pinto de Oliveira, President, Sociedade Brasileira de Malacologia, Instituto de Biologia e de Geociências de Universidade Federal de Juiz de Fora, Minas Gerais, Brazil.

WESTERN SOCIETY OF MALACOLOGISTS. — The 6th Annual Meeting of the Western Society of Malacologists will be held at the Asilomar Conference Grounds in Pacific Grove, California 11-14 July 1973 and will feature contributed papers, symposia, displays and study workshops on molluscan subjects. Inquiries may be sent to the Secretary, Mrs. Edith Abbott, 1264 W. Cienega Ave., San Dimas, California 91773, U.S.A. Applications for membership in the Society should be sent to the Treasurer, Mr. Glenn Burghardt, 14453 Nassau Road, San Leandro, California 94577. Dues are US$ 2.50 for regular members and US$ 1.00 for students. Executive Board Members for the year are: President, Mrs. Twila Bratcher; First Vice-President, Dr. James H. McLean; Second Vice-President, Dr. James Nybakken; Secretary, Mrs. Edith Abbott; Treasurer, Mr. Glenn Burghardt; Members-at-Large, Dr. George Radwin and Dr. George M. Davis; the 3 most recent Past Presidents are Dr. A. Myra Keen, Dr. Eugene V. Coan and Mrs. Beatrice L. Burch.

MOLLUSK SEMINAR AT THE UNIVERSITY OF MICHIGAN, August 1973. — A seminar on various aspects of malacology will be held at the Museum of Zoology, The University of Michigan, on 24 and 25 August 1973. Areas covered will depend on the participants. The seminar will be informal and will consist of a series of brief presentations by participants followed by brief discussions. More extensive discussions may be arranged in subjects of special interest.

Those wishing to attend or to participate in the seminar should contact Dr. J. B. Burch, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE. — The 2nd Congress of the French Malacological Society (Société Française de Malacologie) will be held at Lyon, France (Université Claude Bernard, 43, Blvd. du 11 Novembre, Villeurbanne near Lyon), on 4-8 September 1973. Within the framework of this Congress, two symposia will be held: Malacology in brackish waters (fossil and Recent molluscs); and Neuro-anatomy and neuro-cytology in molluscs. Participants must be members of the Society.

For further information write Mrs. Richardot, "Congrés de Malacologie", Départ. de Biologie animale et Zoologie, 43, Blvd. du 11 Novembre, 69621 - Villeurbanne, France.

UNITAS MALACOLOGICA EUROPAEA. — The 5th European Malacological Congress will be held in Milan, Italy, 2-8 September 1974. For further information contact the Secretary, Dr. Oliver E. Paget, Naturhistorisches Museum, Burgring 7, A-1014, Vienna, Austria, or the President, Dr. Ferdinando Toffoletto, Museo Civico di Storia Naturale, Corso Venezia 55, 20121, Milano, Italy.

* * *

OBITUARY
TOM IREDALE
1880-1972

Tom Iredale, Conchologist at the Australian Museum for 20 years, died on 12 April 1972 at the age of 92.

He freely admitted his first love was ornithology and published extensively in this field, but his most prolific work was on molluscs. He has been responsible for over 2600 new names and over 350 papers.

Iredale immigrated to New Zealand for health reasons and there studied the local molluscan fauna and then, in 1908, spent 10 months on the Kermadec Islands to the north of New Zealand (with W. R. B. Oliver). His experiences with these faunas greatly influenced his later work. From 1909 to 1923 Iredale worked at the British Museum assisting G. M. Mathews in his work *The Birds of Australia* (1910-27, Witherby & Co., London, 12 vols.), but he also wrote papers on molluscan nomenclatural and bibliographic problems and assisted C. D. Sherborn with his *Index Animalium* (1902-33, pt. 1, Cantabrigae, e Typographio Academico; pt. 2, British Museum). He became conchologist at the Australian Museum in 1924 replacing Charles Hedley. Iredale was assisted by Miss Joyce Allan who was responsible for most of his illustrations and who, in turn, became conchologist in 1944 on Iredale's retirement.

While at the Australian Museum Iredale produced valuable lists of the land and freshwater molluscs of the Australian region, a revision of the Australian and New Zealand "loricates" (chitons) with Basset Hull, reports on shells from Sydney Harbour and the N.S.W. continental shelf, and Queensland, as well as many other works.

Iredale was actively publishing in his last years, most of his later papers dealing with bibliographic matters.

Perhaps Iredale's greatest contribution was to his friends and colleagues as he was always a source of inspiration and knowledge and will long be remembered by those that knew him.

A detailed account of Iredale's life and a complete bibliography has been published in the *Australian Zoologist* by Mr. G. P. Whitley (1972, *Aust. Zool.*, 17(2): 65-125).

W. F. PONDER

BOOK REVIEWS

THE AQUATIC AND LAND MOLLUSCA OF TEXAS. E. P. Cheatum & R. W. Fullington. Dallas Museum of Natural History, Bulletin 1. Part One. *THE RECENT AND PLEISTOCENE MEMBERS OF THE GASTROPOD FAMILY POLYGYRIDAE IN TEXAS*, 1971, p 1-74. Supplement, *KEYS TO THE FAMILIES OF THE RECENT LAND AND FRESH-WATER SNAILS OF TEXAS*, 1971, p 1-13.

Part One of "The aquatic and land Mollusca of Texas," entitled *The Recent and Pleistocene members of the gastropod family Polygyridae in Texas*, includes a synonymy, shell description, distribution by county and photographs (3 or more views) for each of the 40 species and subspecies considered, along with an accompanying key. This publication is disappointing since it is little more than an updating for the state of Texas of the *Land Mollusca of North America* (*North of Mexico*) by Pilsbry (1940, Monogr. 3, Acad. natur. Sci. Philad.). Essentially, it is an annotated faunal list of a family of mollusks that has been rather well-studied in the past. The minor taxonomic changes from Pilsbry's monograph are mostly the reshuffling of names as based on shell characters. Unfortunately, Cheatum and Fullington's publication does not deal with phylogeny within the Polygyridae and mentions little or nothing about specific biological considerations of the various species. There are some new distributional records, but to simply record the county of occurrence has only limited value. The shell descriptions, references and synonymies are useful; however, most of this information can be found in Pilsbry (1940) - where the synonymies are more complete, except for the literature references since 1940. Plate 10, Fig. 1 shows 4 electrophoretic gels of 3 *Triodopsis* species and a "hybrid." Apart from the fact that the "hybrid" is not further identified, the illustrations are meaningless because they are accompanied by no explanation of techniques, discussion of methods used to standardize electrophoretic procedures, how many tests were made of each species, what were the limits of variation in banding patterns, what in the authors' eyes constitute "distinct differences," etc. (Although their photographs are poor, it appears that the distances from origin to front in the gels are not uniform.) Yet, the authors conclude that "such tests may be a useful 'tool' in taxonomy." No mention is made of the previous use of electrophoresis in molluscan taxonomy.

The Supplement consists of *Keys to the families of the Recent land and fresh-water snails of Texas*, with selected illustrations of species and a notation of the general distribution in the state for each family. In the introduction, the authors state that among land snail families "...the families Polygyridae and Zonitidae probably have the most widespread distribution over the state." However, in the key, statewide distribution is also cited for the families Philomycidae, Limacidae, Strobilopsidae, Endodontidae, Helicidae, Achatinidae, Succineidae, Carychiidae and Pupillidae. It appears that the authors have confused "widespread distribution" with relative abundance (i.e., frequency and number of populations encountered). In the key to the freshwater snails, the illustration which is labelled *Ferrissia* sp. appears to be an European *Ancylus* species (or, if it is a *Ferrissia*, it is an extremely atypical one). In reference to the Lymnaeidae, one wonders why they use *Pseudosuccinea* as a separate genus, yet place *Fossaria humilis* and *F. bulimoides* in the all inclusive genus *Lymnaea s.l.*

Figs. 1 and 2 (in Part One) and 1, 2 and 3 (in the Supplement) seem to be taken

almost directly or with token alterations from *How to know the Eastern land snails* by J. B. Burch (1962, Wm. C. Brown Co., Dubuque, Iowa, 214 p). Yet, Burch receives no acknowledgment or literature citation in either of these publications, even though Texas land snails are included in Burch's handbook.

These Texas publications will undoubtedly be of some value to those studying Texas non-marine shells since they add some new distribution records, and consolidate the more recent information on Texas Polygyridae.

C. M. PATTERSON

Museum of Zoology
University of Michigan
Ann Arbor, Michigan 48104
U. S. A.

Malacological Review, 1973, 6: 83-100

CONTENTS OF CURRENT MALACOLOGICAL PERIODICALS

The contents of current malacological periodicals, as shown by their tables of contents, are herewith reproduced (with permission) as a service to the scientific community. The journals are listed in chronological order of date of founding. Also listed are editors and editorial offices (footnotes). Those journals that do not have their contents printed in this current issue of *Malacological Review* (Vol. 5, No. 2) are marked by an asterisk in the right hand column below; contents of these journals will be included in future issues of *Malacological Review*.

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1850	*Journal de Conchyliologie*	P.-H. Fischer[4]	*
1868	*Archiv fiir Molluskenkunde*	A. Zilch[5]	*
1874	*The Journal of Conchology*	N. F. McMillan[6]	*
1886	*The Nautilus*	R. T. Abbott[7,**]	*
1893	*Proceedings of the Malacological Society of London*	A. Graham[8]	84
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1932	*The American Malacological Union, Inc., Annual Reports*	M. K. Jacobson[11]	*
1936	*Basteria*	W. S. S. van der Feen-van Benthem Jutting[12,†]	*
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[1]Year for which the journal was first published.

[2]Prominent shell collectors' magazines may be included in future numbers of *Malacological Review*.

[3]Footnotes 4-23 list the main editorial offices of the various journals.

[4]18/55 Prince Albert St., Mosman, N.S.W. 2088, Australia.

[5]Senckenbergishchen Naturforeschende Gesellschaft, Senckenberg-Anlage 25, 6 Frankfurt 1, Germany (FR).

[6]The Nook, Uplands Rd., Bromborough, Cheshire, U.K.

[7]Delaware Museum of Natural History, Greenville, Delaware 19807, U.S.A.

[8]Department of Zoology, The University, Whiteknights, Reading RG6 2AJ, U.K.

[9]National Science Museum, Ueno Park, Taito-ku, Tokyo, Japan.

[10]National Marine Fisheries Service, Oxford, Maryland 21654, U.S.A.

[11]3957 Marlow Court, Seaford, New York 11783, U.S.A.

[12]Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands.

[13]3 Nantes Street, Newtown, Geelong, Victoria 3220, Australia.

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OF LONDON

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[18]Viale Piceno 39, Milano, Italy.
[19]Via De Sanctis, 73, Milano, Italy.
[20]Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.
[21]1217 Waller Street, San Francisco, California 94117, U.S.A.
[22]P.O. Box 9216, Haifa, Israel.
[23]55, Rue de Buffon, Paris 5e, France.

*Contents not included in this number of *Malacological Review* because current issues have not yet been received.

**Co-editor, C. B. Wurtz.
†Co-editor, A. C. van Bruggen.
††General Editors, A. Gismann and C. J. Bayne.
[x]With editorial committee.
[xx]With editorial committee.
[+]Associate Editor, C. M. Patterson.
[++]Edited by the Société Française de Malacologie.

VENUS

THE JAPANESE JOURNAL OF MALACOLOGY

第30巻 第4号 Vol. 30, No. 4

昭和47年2月 February 1972

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本部移転：

本年から学会本部が下記のように移転しましたので御注意下さい。

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新住所：東京都新宿区百人町3—23—1
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電話東京（03）364—2311（代表）
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外国会員：10米ドル又は3.5英ポンド

創立45周年大会：

昭和48年は日本貝類学会創立45周年にあたるので，同年5月4日～7日に45周年大会が東京で開かれます。（会場未定）。又，これと時期を合わせて日本橋東急デパートで貝類展も開催されます。詳細は追って会誌上でおしらせします。

IMPORTANT NOTICES

HEAD OFFICE MOVED:

The Head Office of Malacological Society of Japan moved as follows:

Old address: c/o National Science Museum, Ueno Park, Taito-ku, Tokyo.

New address: c/o National Science Museum (Natural History Institute) 3—23, Hyakunin-cho, Shinjuku-ku, Tokyo.

SUBSCRIPTION FEE CHANGED:

The subscription fee was changed with an approval of general session for 1972 as follows:

Foreign members: 10 U.S. Dollars or 3.5 British Pounds per annum.
Domestic members: 1700 Yen per annum.

ANNOUNCEMENT FOR THE 45TH ANNIVERSARY MEETING:

The 45th Anniversary Meeting of the Malacological Society of Japan will be held at Tokyo in the period from May 4 to 7, 1973. The detailed information will be given later.

VENUS

THE JAPANESE JOURNAL OF MALACOLOGY

第31巻 第2号 Vol. 31, No. 2

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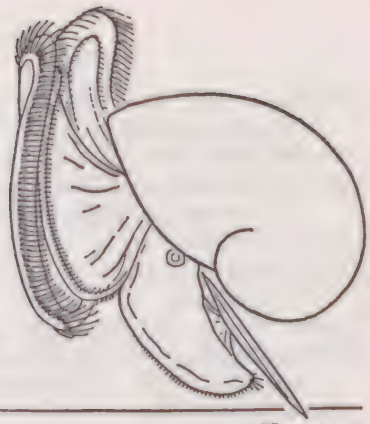

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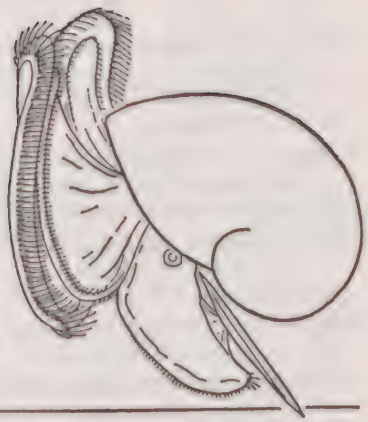

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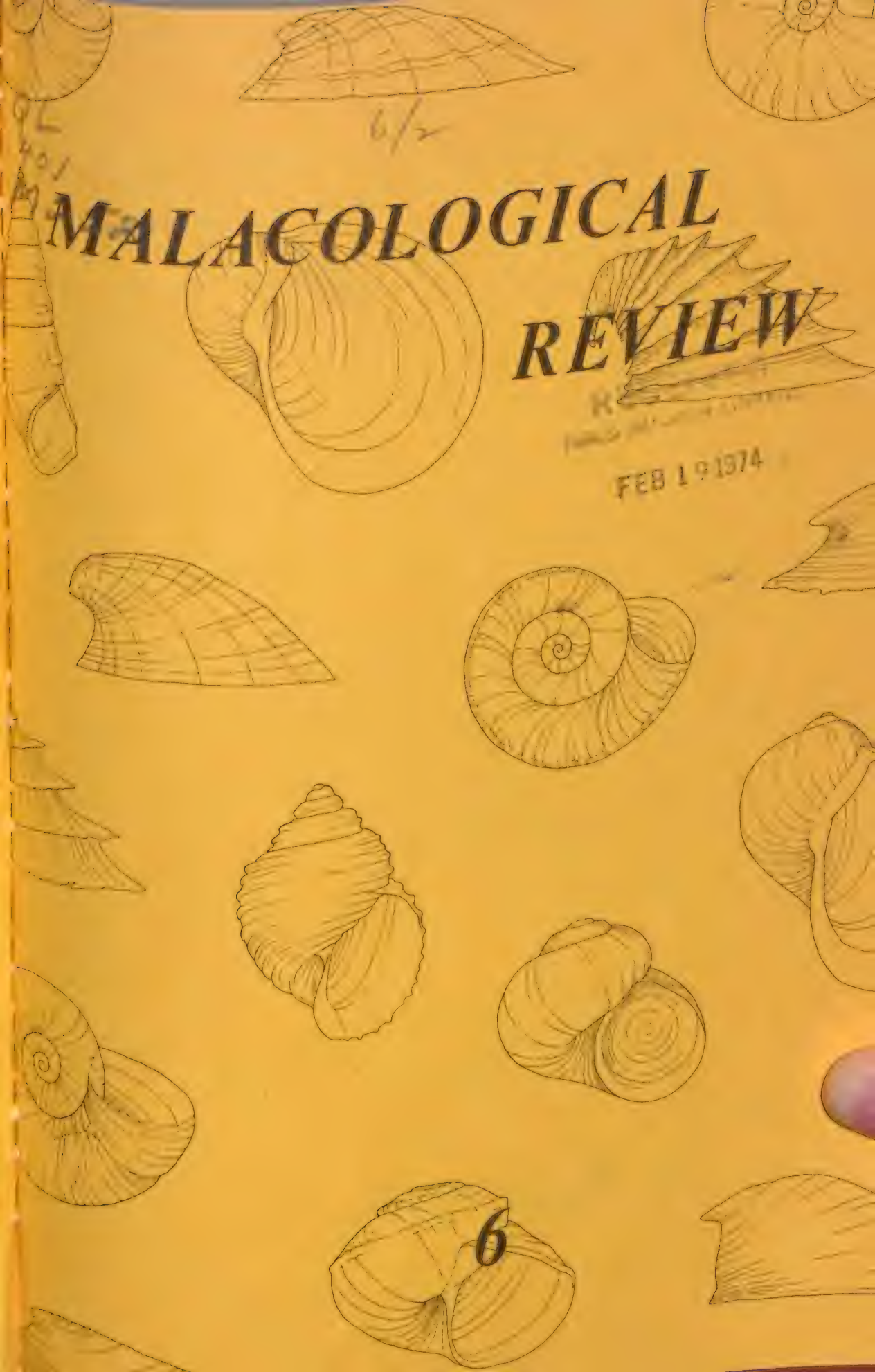

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ON THE COVER - Freshwater gastropod mollusks of the Lake Ohrid region, Macedonia, Yugoslavia. Illustrations by Carole W. Christman.

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Vol. 6: Freshwater gastropods of the Lake Ohrid region, Yugoslavia

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Malacological Review, 1973, 6: 105-117

FUSCONAIA MASONI (CONRAD 1834) (BIVALVIA: UNIONACEA) IN THE ATLANTIC DRAINAGE OF THE SOUTHEASTERN UNITED STATES

Samuel L. H. Fuller

ABSTRACT

Fusconaia masoni (Conrad 1834), previously reported from the Savannah River system in Georgia and the Cape Fear River system of North Carolina, also occurs in the Ogeechee River system of Georgia. These are the first unequivocal records of this genus in the Atlantic drainage of eastern North America. A redescription of *F. masoni* is accompanied by discussions of its ecology, systematic relationships and zoogeography. Particular attention is paid to the systematic status of the closely allied genus *Lexingtonia* Ortmann 1914 and to the difficulty of classifying these genera and their relatives in any existing system of the Unionacea. The 2 genera (or their ancestors) probably entered the southern Atlantic drainage during confluence of the ancient Roanoke and Teays Rivers.

INTRODUCTION

Recent collections of freshwater mussels from the southeastern United States include specimens which conform to the concept of *Fusconaia* Simpson 1900 as advanced by Ortmann (1912: 239, 1919: 6). This material constitutes the first intimation that this genus occurs in the Atlantic drainage of eastern North America since Simpson (1900: 785; 1914: 868), unavoidably ignorant of its anatomy and beak sculpture, hesitantly placed *Unio pumilus* Lea 1838 from the Cape Fear River system of North Carolina in his section *Fusconaia* of the genus *Quadrula* Rafinesque 1820. Following Fuller (1971, 1972), this species is here referred to *Unio masoni* Conrad 1834 from the Savannah River system of Georgia and South Carolina, the earliest available and conchologically appropriate taxon whose type locality lies within the range of this species as currently understood. This species has occasionally been reported in the literature as a member of the genus *Pleurobema* Rafinesque 1819 or the genus *Lexingtonia* Ortmann 1914 (usually as *L. subplana* (Conrad 1837)).

Much of the present paper is devoted to a redescription of *Fusconaia masoni* (Conrad 1834), with notes on its ecology and systematic relationships, but of equal interest are the zoogeographic implications of these first unequivocal records of *Fusconaia* in the Atlantic drainage of the United States and Canada. Accordingly, the origins of *Fusconaia* and *Lexingtonia*, the nature of their close relationship, and the role of former stream confluence in their penetration of the Atlantic drainage are explored in some detail.

TERMINOLOGY AND PROCEDURES

Abbreviations: ANSP = Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A. MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. USNM = United States National Museum [National Museum of Natural History, Smithsonian Institution], Washington, D.C., U.S.A.

Terminology: The expression *tetragenous* will be used in this paper to denote mussels having marsupial structure in all demibranchs of the (female) gills; *digenous* will refer to those whose marsupial structure is restricted to the outer demibranchs.

The expression *fusconaiad* will refer to the unionine genera with subcylindrical egg masses (e.g., Figs. 5-7). Fusconaiad bivalves are *Fusconaia* (Ortmann, 1912: 239), *Lexingtonia* (Ortmann, 1914: 29; 1921: 84) and *Quincuncina* Ortmann 1922 (Ortmann, *in* Ortmann & Walker, 1923: 2). *Cyclonaias* Pilsbry 1922 is a possible 4th fusconaiad genus, since Ortmann (1919: 57-58) described subcylindrical egg masses in the outer demibranchs of *Rotundaria* [=*Cyclonaias*] *tuberculata* (Rafinesque 1820) and noted that its beak sculpture is a combination of the concentric, double-loop and zigzag types. Similar sculpture is also found in *Quincuncina* (Ortmann & Walker, 1923: 2-3).

Sterki (1898: 19, 28-29) described "cylindrical" egg masses from certain *Unio* now placed in *Strophitus* Rafinesque 1820 and *Cyprogenia* Agassiz 1852, but additional peculiarities of the egg masses, marsupia and other characters consign these genera to Ortmann's (1910, 1911, 1912) concepts of the subfamilies Anodontinae and Lampsilinae, respectively.

Collection and preparation of material: Most specimens were taken by hand and insensitized in 2 or 3 days' time with a Nembutal solution of less than 1% by volume in tap water (a variation of the method of van der Schalie, 1953). In the absence of a better fixative, the Cape Fear River specimens were killed and graded up in ethanol to a storage strength of 70% ethanol by volume, with minimal distortion of the soft parts. All other material was fixed in a formalin solution of about 5% by volume in tap water before storage in ethanol.

Both demibranchs of the left gill in every specimen were examined with transmitted light under 10X-60X power of a Bausch & Lomb dissecting microscope. The gill wall was teased away to reveal the structure and spacing of the interlamellar septa. The material has not been examined for histological evidence of the hermaphroditism known to occur in some *Fusconaia* (Sterki, 1898: 31; van der Schalie, 1970: 95).

Material examined: All specimens of *Fusconaia masoni* used in this study are deposited in the alcoholic collections of the Department of Malacology at the Academy of Natural Sciences of Philadelphia. Three populations were sampled:

1) Cape Fear River system: Cape Fear River drainage. Cape Fear River, 0.1 mile downstream from confluence with Carvers Creek, about 3 miles southwest of Slocomb and about 6 miles north-northeast of Fayetteville, Cumberland County, North Carolina. ANSP A2267 — 2 females; 19 September 1969; S. L. H. Fuller, collector. ANSP A2268 — 2 males; 11 June 1970; S. L. H. Fuller, collector. ANSP A2269 — 6 females (3 ovigerous); 11 June 1970; S. L. H. Fuller, collector.

2) Savannah River system: Brier Creek drainage. Mill Race at Georgia state route 23, about 2 miles north of Sardis, Burke County, Georgia. ANSP A2263 — 3 females (all ovigerous); 8 July 1971; S. L. H. Fuller, collector. ANSP A2264 — 1 male; 8 July 1971; S. L. H. Fuller, collector. ANSP A2265 — 2 females (1 ovigerous); 18 July 1971; S. L. H. Fuller, collector.

3) Ogeechee River system: Buckhead Creek drainage. Magnolia Springs outfall, about 3 miles south-southwest of Perkins, Jenkins County, Georgia. ANSP A2266 — 2 females (1 ovigerous); 18 July 1971; J. W. Richardson, collector.

RESULTS

Redescription of *Fusconaia masoni*: The shell is rather small, at least 64 mm (about 2 1/2 inches) in length; it is sub-rhomboid in outline, thin but strong, of rather great height (ranging from about 3/5 to about 4/5 of the length), moderately inflated (width about 2/5 of the length) and without apparent sexual dimorphism. The beaks are slightly prosogyrous, prominently elevated above the dorsal margin and located anteriad of center. The beak sculpture consists of 3 or 4 subconcentric bars of about equal weakness, almost straight and very weak across the disk, obsolete anteriorly and weakly tuberculate at the posterior ridge, where they turn sharply dorsad and quickly disappear. Later bars are no more than weak tubercles at the ridge. The adult shell is without sculpture. The brownish-yellow periostracum, sometimes partially obscured by foreign deposits, is decorated with concentric low folds and ridges, which presumably mark the ends of growth periods.

The posterior ridge is prominent and broadly rounded. The posterior slope is weakly concave and usually scored by 2 shallow grooves subparallel to the ridge, which cause little or no biangulation of the posterior margin. The hinge is yellowish-brown, rather broad, opisthodetic, short (about 1/4 of the shell length) and raised prominently above the dorsal margin for most of its length.

The dorsal margin descends posteriorly; before the beaks it is short, often descendant, and usually forms an obtuse but distinct angulation with the anterior margin, which is often very nearly straight. The ventral margin is an even,

shallow curve which meets the dorsal margin in a blunt point just below the mid-line. Older individuals may be slightly produced post-basally.

The hinge plate is rather narrow, extending about 1/2 of the shell length. The interdentum is short and (for a *Fusconaia*) very narrow. The nymphal callosities are conspicuous bars, about 1/2 of the length of the lateral teeth, which project sharply dorsad. The laterals are short (about 1/3 of the shell length), straight or very slightly decurved, blade-like and, descendant in the rear, set obliquely to the dorsal margin. There is one lateral in the right valve; 2 in the left, of which the lower is somewhat longer and more broad. There are 2 pseudocardinal teeth in the left valve; each is irregularly sub-deltoid, strong and conspicuously subdentate on its dorsal surface. The posterior tooth is sub-umbonal and the more strongly developed and subdentate. There is one pseudocardinal in the right valve and often a vestige of a sub-umbonal tooth on the interdentum. The right pseudocardinal is larger, longer and usually more peg-like than those of the left valve and is not subdentate. The interlocking surfaces of all teeth are variably rugose (particularly the pseudocardinals) or finely ribbed (particularly the laterals); rugosity extends onto the right interdentum.

The nacre is smooth throughout, with no unusual sulcations. The beak cavity is deep. The pallial line is narrow and faintly impressed; it forms an even curve subparallel to the shell margin, except for an occasional shallow concavity at the postbasal corner of the posterior adductor muscle scar. The anterior muscle scars are impressed, particularly along their posterior margins, but the posterior scars, although clearly outlined, are scarcely or not impressed. The dorsal muscle scar is an oblique grooved ridge on the interdentum within the beak cavity. The nacre is thickened and white over about the anterior 2/3 of the shell, especially at the bases of the pseudocardinal teeth and below and before the pallial line. The nacre becomes iridescent posteriorly and is often so thin that the growth rests in the periostracum show clearly through.

The free mantle margins are trilobate and undifferentiated, except at the anal and branchial apertures. The branchial bears 2 somewhat intermingled rows of papillae. Those of the inner row rise subapically from the inner lobe; they are longer, stouter, sub-tentaculate, fused to the mantle baso-laterally and spaced unevenly and discontiguously for the most part. Ordinarily they terminate simply, but biramous individuals are common; rarely the form is dendritic, with as many as 5 processes. Papillae of the outer row rise apically from the inner lobe; they are much shorter, more slender, comparatively stiff, scarcely fused to the mantle baso-laterally, arranged closely and at rather equal intervals and simple. In life the inner papillae are erected obliquely from the mantle and almost interdigitate across the branchial aperture; the outer papillae lie sub-parallel to the mantle, projecting posteriad. The papillae of the anal aperture resemble those of the outer branchial row; their disposition in 2 rows is obscure.

The branchial and supra-anal apertures approach twice the length of the anal. Although in life the inner lobes of the apposing mantle margins lie tangentially between the anal and branchial apertures (effecting their functional separation), there is no mantle fusion between them. There is a high and strong fusion of the inner lobes between the anal and supra-anal apertures. A similar connection closes the supra-anal dorsally for much of its height, and the remaining opening may be broken up by one or more additional fusions.

The inner demibranch is the greater in length and height; it hangs slightly below the outer behind and greatly below anteriorly, and it extends farther anteriad. Sweeping sharply dorsad, its anterior margin is truncate. Anteriad of the posterior margin of the foot, the dorsal margin of the inner demibranch is free of the

visceral mass, excepting a brief attachment anteriorly. The ventral margin of the inner demibranch is thickened and grooved; in the outer demibranch it is thin and sharp. Male water tubes comprise about 12 gill filaments; female, about 6. Male septa are delicate, the thickness being no more than the breadth of a single filament. Female septa are sturdy, with a thickness equal to the combined breadths of several filaments.

Both demibranchs are marsupial in the female. Egg masses occur in all water tubes of the ovigerous female, excepting a few lying farthest anteriad and posteriad. These uncharged regions may be more extensive in the inner demibranch. Egg masses extend most of the height of the water tubes. They are very sturdy; aborting under stress, some may break transversely, but their natural form is otherwise retained. There are about 30 to 50 sub-cylindrical egg masses in each demibranch. Ten strands of ova can usually be distinguished at the midpoint of the egg mass, where a layer of 4 strands is sandwiched between 2 layers of 3 strands each; in other words, 8 strands are more or less equally spaced around, and parallel to, the remaining 2. At its midpoint the mass is suboval in cross sectional outline, but, where the strands intermingle at the dorsal and ventral ends of the mass, 6 strands are often ranged more or less circularly and hexagonally about a central seventh. The egg is subspherical, variable in diameter (about 0.15 to 0.20 mm in preservation), translucent, with a subcentral opaque embryo, usually vividly pigmented with a red or orange-red color. The marsupia are slightly swollen; the outer one retains the sharp distal margin of the demibranch. The glochidium is unknown.

Outer oral palpi are larger than the inner; posterior margins of the palpi are fused for about the proximal 1/3 of their lengths. The palpi are sub-falciform in outline, longitudinally grooved on their apposing surfaces, bluntly attenuate distally and slightly overlap the anterior margins of the inner demibranchs.

Adductor muscles are irregularly sub-oval in cross section; the pedal retractors are tiny. The pallial musculature is thick and extensive. The dorsal muscles are short, strong bars set obliquely on the apposing surfaces of the mantle within the beak cavities. The foot is rather long and slender, curving slightly dorsad in life. The posture of the anal hood forces discharge ventrad into the suprabranchial cavity before the anal aperture; the hood has reflected lips with scalloped margins. The dorsal crest of the mantle between the lateral teeth is short, very high, and subrectangular in lateral outline.

Most of the animal is a soiled or yellowed white (the coloration intensified in preservation). In life, regions of heavy musculature are comparable to the ova in color; these include the pedal, pallial, adductor, papillary, and pedal protractor and retractor muscles. The mantle is darkly mottled among the bases of the papillae. A band of similar pigment lies sub-parallel to the mantle margin a short distance before the branchial papillae. Dark mottlings may occur about the animal generally.

Habitat: All Cape Fear River specimens of *Fusconaia masoni* were secured immediately downstream of a jam of fallen timbers and brush, which broke the current so that a sheltered, shallow area was created with a sand, mud and silt bottom. These conditions are at variance with the optimum for Mississippi basin *Fusconaia*, which, according to numerous authorities, prefer substrates of gravel or hard sand, often in swift and deep waters. Nonetheless, the Cape Fear material is less conchologically depauperate than specimens from Mill Race in the Savannah River system which is a tiny creek with a predominantly sand bottom. Specimens from the Magnolia Springs outfall in the Ogeechee River system were far larger and heavier than those at the latter 2 localities. The abundance of

pleurocerid snails in the outfall is another indication that this water is relatively pristine, well oxygenated and rich in calcium. Clearly, radical adjustment in habitat tolerance was involved as *Fusconaia* spread to the Atlantic drainage.

Host: Coker *et al.* (1921: 152-153) reported centrarchid and anadromous clupeid fishes as hosts of certain Mississippi basin *Fusconaia*, but the hosts of other members of the genus, including *F. masoni*, are unknown. Since the genus is so widespread, there is no reason to assume that Atlantic drainage hosts are related to those employed in the Mississippi basin in any way other than ecological suitability.

Parasites: Although infestation with *Unionicola* was commonplace among some naiad species associated with *Fusconaia masoni* (especially in the Cape Fear River), evidence of infection with neither water mites (Arthropoda: Acari: Unionicolidae) nor "distomids" (Platyhelminthes: Trematoda: Digenea) has been found in the *F. masoni* examined.

DISCUSSION

Systematic relationships

Superfamily: Although the larva of *Fusconaia masoni* is unknown, it is safe to assume that, as in other *Fusconaia*, the larva is a glochidium (see, e.g., Ortmann, 1919: 19). Accordingly, *F. masoni* is best placed in the superfamily Unionacea (see Heard & Guckert, 1971), but the correct family for this genus and species is uncertain.

Family: The better unionacean classifications, i.e., those of Ortmann (1910, 1911, 1912) and of Heard & Guckert (1971), based on imaginative analyses of a wide variety of somatic and reproductive characters, do not emphasize the role of ancestral fusconaiad mussels in a history in which one of the turning points among non-hyriid unionaceans was restriction of marsupial function to the outer demibranchs. This development, however, would have been a disaster had there not already begun a tendency toward the "elastic" marsupium, a device which permitted a reduction in the number of marsupial demibranchs without jeopardizing reproductive capacity. This chronology is reflected in genera like *Quadrula*, whose elastic marsupia accomodate broad egg masses, but which has not relinquished the marsupial function of the inner demibranch. Similarly, the tetragenous genera *Fusconaia* and *Quincuncina* reflect an intermediate stage in the development of marsupial elasticity, where a more narrow egg mass (i.e., the subcylindrical type) is necessitated by water tubes whose septa are capable of only moderate lateral extension. The genus *Lexingtonia* is the only surviving representative of one of the stocks whose marsupial demibranchs were reduced in number before adequate marsupial elasticity was realized; the relict distribution of this genus (see below) emphasizes the consequences of the lowered reproductive potential explicit in this unfortunate evolutionary experiment. Thus it appears that the elasticity of marsupial demibranchs has had greater biological significance than has had the number of them. I further suspect that, in most unionine stocks, marsupial elasticity had been developed before the number of marsupial demibranchs was reduced.

From the genetic point of view, the latter conclusion is an aprioristically logical one. The genetic change involved in the genesis of the elastic marsupium would be minor in that greater elasticity is effected merely by increasing the quantity of a single type of tissue (see Ortmann, 1911: 291). Loss of marsupial function in a demibranch, however, is a more complex, essentially qualitative adjustment, because the demibranch would have to be restructured and the ova

prevented from entering it. This would be a major genetic undertaking. Increased marsupial elasticity could easily and advantageously have developed at any time, regardless of whether or not reduction in number of marsupial demibranchs was happening concurrently, but the latter development was ever a disadvantage without the former.

If it is assumed that chronologically (not morphologically) primitive characters best reflect natural relationships, then among most (if not all) surviving unionine groups, marsupial incubative capacity is a systematic character more significant than the number of marsupial demibranchs. Accordingly, use of the latter character in the Heard & Guckert (1971) system as a discriminant between and among families is suspect. Specifically, in placing *Fusconaia* and *Quincuncina* in the tetragenous Amblemidae and *Lexingtonia* in the digenous Unionidae, Heard & Guckert have disguised what I feel is a much closer relationship among the 3 genera. In placing all 3 close to one another in the same subfamily (i.e., Unionidae: Unioninae), Ortmann was, I suspect, much closer to the truth. I would prefer, in addition, to see the fusconaid stage in unionacean evolution given taxonomic recognition at some supra-generic rank, much as Heard & Guckert, in recognizing an amblemid subfamily Gonideinae, have also recognized the stage in the development of the interlamellar septum that is reflected in the dorsally perforate septa of *Gonidea angulata* (Lea 1838) of the western United States and Canada (Ortmann, 1916). Creation of a new subfamily or tribe for the fusconaiad genera seems warranted. Formal introduction of such a taxon, however, is beyond the scope of the present study, whose primary goal is not to gather materials toward another higher unionacean classification.

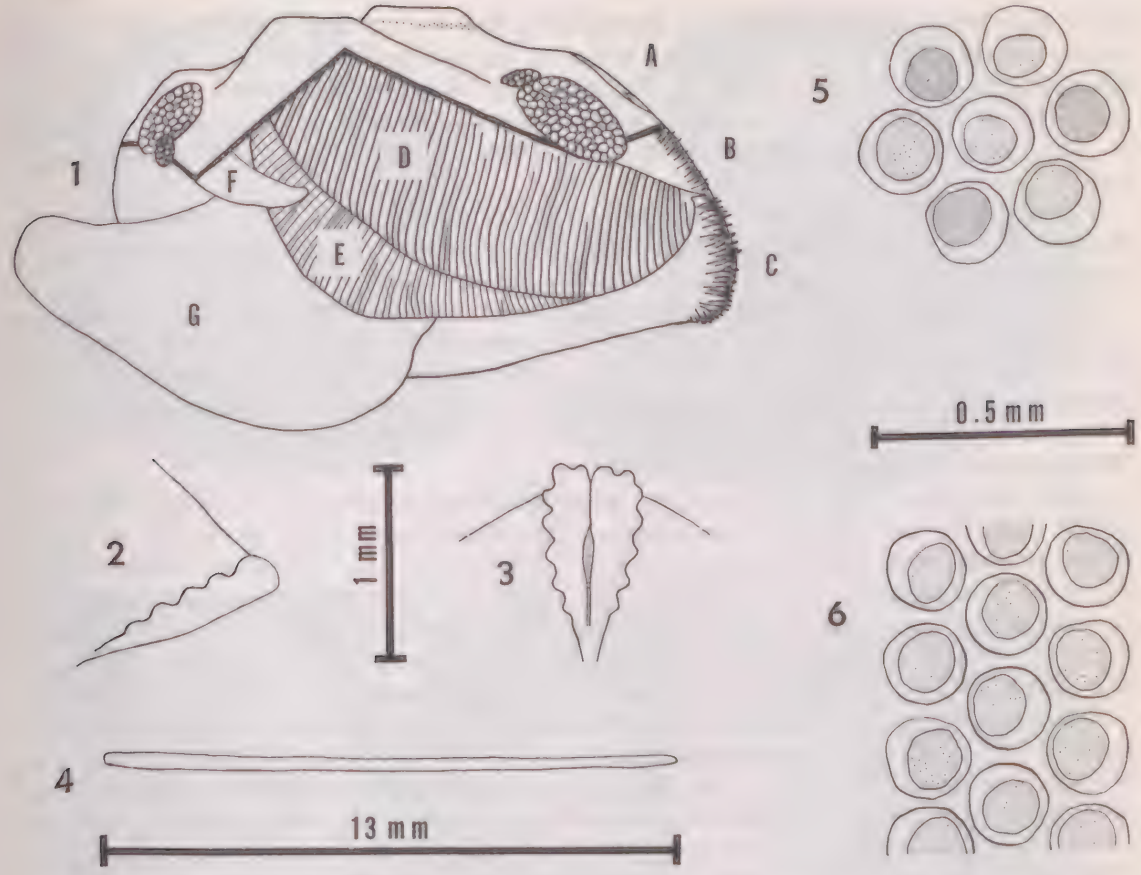
Subfamily: In the Ortmann system of the naiades, *Fusconaia masoni* would be placed in the Unioninae, because gill structure undergoes no qualitative changes during the breeding season; for example, the sharp distal margins of the outer demibranchs remain so when the organism is gravid (Fig. 11). Although the feature is not universal among unionine genera, it should be added that the *F. masoni* breeding season appears to be short: ovigerous females were secured 11 June, but those taken 19 September were barren.

Genus: *Fusconaia masoni* is a fusconaiad mussel by virtue of its subcylindrical egg mass (Figs. 5-7) and water tubes. *Lexingtonia* is the only genus which can be confused with *Fusconaia*, but the latter has less well developed beak sculpture (Table 1, Fig. 10) and the tetragenous marsupial condition (Table 1, Fig. 11). Although there are cases of a digenous mussel's displaying ova in both demibranchs, this condition rarely involves tetragenous marsupial structure (Ortmann, 1919: 71). Since all known females of *F. masoni* have tetragenous marsupial structure, this species should not be thought an atavistic *Lexingtonia*. Apparently the only fusconaid genus in the Apalachicola River system, where it is endemic, (the tetragenous) *Quincuncina* can be distinguished from either genus on account of its remarkable shell sculpture.

Fusconaia masoni has additional peculiarities characteristic of — but not confined to — the genus. The shell is sub-rhomboidal in lateral outline, the posterior ridge is well developed, and umbones are raised well above the lateral margin (Figs. 8-9). The palpi extend somewhat beyond the truncate anterior margins of the inner demibranchs (Figs. 2, 11), and the branchial papillae are dendritic for the most part (Fuller, 1971). Much of the musculature and reproductive tissue is highly colored in life.

Specific identity: Referral of Atlantic drainage *Fusconaia* to *Unio masoni* Conrad 1834 of the Savannah River system is discussed by Fuller (1972).

Intrageneric relationships: Juveniles of *Fusconaia escambia* Clench & Turner



FIGS. 1-6. *Fusconaia masoni* (Conrad 1834), ♀, ANSP A2269, Cape Fear River, 0.1 mile downstream from confluence with Carvers Creek, about 3 miles SW of Slocomb and about 6 miles NW of Fayetteville, Cumberland County, North Carolina, 11 June 1970. 1, Animal, left lateral view with mantle removed at adductor muscles and along heavy line. A-C, supra-anal, anal and branchial apertures, respectively. D-E, outer and inner demibranchs, respectively. F, outer oral palpus. G, foot. 2X. 2-3, Anal hood, lateral and posteroventral views, respectively. 4, Egg mass. 5, Egg mass, transverse cross section near dorsal or ventral end of egg mass as shown in Fig. 4. 6, Egg mass, lateral view near longitudinal midline.

TABLE 1. Contrasting features of *Fusconaia* and *Lexingtonia* (Ortmann, 1912: 239; 1914: 29; 1919: 6; 1921: 84; Boss & Clench, 1967: pl. 15, fig. 1).

Character	Genus	
	Fusconaia	*Lexingtonia*
Beak sculpture	3-4 weaker bars	6-9 stronger bars
Marsupium	tetragenous	digenous

1956 resemble Atlantic drainage fusconaids, but the adult *F. escambia* is so high as to be almost square, and its shell is far more solid, with a massive hinge plate (Clench & Turner, 1956: pl. 7, figs. 3-4). Known only from the Escambia and Yellow Rivers of the eastern Gulf drainage (Johnson, 1969: 35), *F. escambia* is more reminiscent of *Fusconaia* of the western Gulf drainage and the Mississippi basin.

Fusconaia masoni is conchologically unlike *F. succissa* (Lea 1852), which is rather widespread in the eastern Gulf drainage west of the Apalachicola River system (Clench & Turner, 1956: 151-152, pl. 7, fig. 5). The vivid coloration in reds and oranges of musculature and reproductive tissues of *Fusconaia* in general is muted in the occasional *F. succissa*, which may be extensively flushed with browns and blacks (Ortmann, 1923: 74). This darker pigmentation occurs in *F. masoni* and is commonplace in the group of *F. barnesiana* (Lea 1838) of the upper Tennessee River drainage (Ortmann, 1917: 61-62). Possibly these 3 forms constitute a natural group within the genus.

Unio utriculus Lea 1845 is the other Carolinian mussel placed by Simpson (1900: 787) in his section *Fusconaia*. The shell (Lea, 1848: pl. 1, fig. 3) bears little resemblance to a fusconaiad, and Simpson (1914: 787) later referred this form to *Pleurobema*. Lea (1848: 69) wrote that his original specimens came "...from North Carolina, and no doubt from one of the tributaries of the Tennessee River." Johnson (1970: 300) agreed that *utriculus* is not of the Atlantic drainage. The species' generic position is uncertain because its anatomy remains unknown.

Finally, I must call attention to the similarity between *Fusconaia flava* (Rafinesque 1820) of the Mississippi basin and less depauperate populations of *F. masoni* (such as the one in the Magnolia Springs outfall). The similarity is so striking as to provoke the suspicion that these 2 taxa are conspecific, *F. masoni* being only the Atlantic drainage form of *F. flava* and expressing the latter's conchological character in only the most favorable habitats.

Similar species: Aside from the occasional similarity to *Fusconaia flava*, *F. masoni* is conchologically closest to Atlantic drainage populations of *Lexingtonia*. As discussed above, characters of the beak sculpture and soft anatomy (Table 1) will separate the genera in question, but excellent material is required. These features of most museum specimens are destroyed; this has led to the perennial confusion of *Lexingtonia* with other genera (rarely with *Fusconaia*) and to the failure to recognize *F. masoni* as a unique entity.

Status of *Lexingtonia*: As indicated above, I view *Fusconaia* and *Lexingtonia* as distinct genera representing fundamentally different lines of naiad evolution. On the other hand, we but imperfectly understand the evolutionary history of North American Unionacea. Since mussels exhibit few variable morphological features, generic concepts commonly depend upon very few characters. We lack additional data (histological, cytogenetic, immunological) which might extend or reject some of the many concepts that are currently recognized. A broader concept of *Fusconaia*, for example, might reasonably embrace subgenera *Fusconaia s.s.* and *Lexingtonia*. In any case, no viewpoint which recognizes the clear biological differences between *Fusconaia* and *Lexingtonia* would discredit the zoogeographic ideas advanced below.

Frierson (1927: 44) and Johnson (1970: 300) interpreted *Lexingtonia* as a subgenus of *Pleurobema* which has a compressed egg mass (Ortmann, 1919: 71). As long as reproductive characters are thought to be conservative, the nature of the egg mass should be accorded diagnostic value at the generic level, at least. Identification of *Lexingtonia* with *Pleurobema* involves a broad generic concept which obscures important biological differences. Were there supporting evidence

FIGS. 7–10. *Fusconaia masoni* (Conrad 1834), ♀, ANSP A2269, Cape Fear River, 0.1 mile downstream from confluence with Carvers Creek, about 3 miles SW of Slocomb and about 6 miles NW of Fayetteville, Cumberland County, North Carolina, 11 June 1970. 7, Animal, ventral view with mantle reflected dorsad. a, papillae of left branchial aperture. b, ovigerous left outer demibranch (note sharp distal margin). c, ovigerous right inner demibranch. d, right outer oral palpus. e, foot. f, left mantle. 1.25X. 8, Length 39.0 mm, height 27.5 mm, width 16.5 mm. Age about 10 years. 1.25X. 9, Length 53.0 mm, height 33.5 mm, width 20.0 mm. Age about 13 years. 1.25X. 10, Beak sculpture. Asymmetrically disposed and developed annuli 4–5 probably are not true juvenile umbonal bars. 6.25X.

from a variety of disciplines, the entire system of Ortmann's (1910, 1911, 1912) Unioninae might be overhauled to advantage. Unfortunately, the conservative approach based only upon certain (usually conchological) characters has not been consistently applied. For instance, Johnson and Frierson both distinguished between *Pleurobema* and *Elliptio* Rafinesque 1820, whose similar egg masses (Ortmann, 1912: 263, 269, 271) imply closer relationship than exists between *Pleurobema* and any fusconaiad genus.

Zoogeography

Fusconaia has invaded previously glaciated areas to a lesser extent than ecologically comparable genera like *Pleurobema*. Although rather common in the Lake Ontario drainage (Harman, 1970), *Fusconaia* evidently has failed to become established in the St. Lawrence River system; early St. Lawrence records (as in Simpson, 1900) apparently depended upon confusion with *Pleurobema*. *Fusconaia* does not occur elsewhere in the Atlantic drainage north of the terminal moraine (numerous authorities). Recognition of *F. masoni* in the Cape Fear, Savannah and Ogeechee River systems confirms occurrence of the genus in the Atlantic drainage south of the moraine. *Fusconaia* has been reported throughout the Mississippi basin and the Gulf drainage (numerous authorities).

It is unlikely that absence of *Fusconaia* from the Apalachicola River system (Clench & Turner, 1956: 106) is due to extinction, because of the rich naiad fauna revealed by them. Accordingly, it is certain that *Fusconaia* did not reach the Atlantic drainage through the generally accepted confluence of Savannah River system headwaters with those of the Chattahoochee River, a major tributary of the Apalachicola in northwestern Georgia. Although the fusconaid genus *Quincuncina* is represented in the Apalachicola system, it is inconceivable that even a remarkable depauperization could have realized *F. masoni* from an ancestor close to the heavily sculptured *Quincuncina*. Limited fossil evidence bears only negatively on these points: La Rocque (1967: 169) recorded a single naiad (possibly *Lampsilis* Rafinesque 1820) from Pleistocene deposits at Ladds in Bartow County, northwestern Georgia, within the Etowah River watershed of the Coosa-Alabama River system.

There are certain avenues and mechanisms of dispersal which have *not* afforded *Fusconaia* any access to the Atlantic drainage. (1) Modern *Fusconaia* clearly did not enter the Atlantic drainage during the presumed confluence of the Susquehanna River system with headwaters of the Monongahela River in the Ohio River drainage of central Pennsylvania (see Ortmann, 1913: 368-371). (2) According to Pilsbry (1897), fossil mussels from Pleistocene (Henderson, 1935: 94) deposits near the Delaware River at Fish House in Camden County, southern New Jersey, include no fusconaiads and show affinities to the modern Great Lakes fauna. Simpson (1894) reported no fusconaiads among fossil mussels from Toronto, Canada. There is, then, no indication that fusconaiads have ever inhabited the Atlantic drainage north of the terminal moraine. (3) Mesozoic or early Tertiary invasion of Virginia, the Carolinas and Georgia by ancestors of modern Atlantic drainage fusconaiad genera is unlikely, because the present fauna reflects nothing of the inevitable radiation of so ancient a stock. (4) Human introduction of glochidially infected host fish is out of the question, because fusconaiad mussels were being described from the Atlantic drainage long before inauguration of fish stocking at the close of the last century (Cornell, pers. comm.) as an aid in wildlife management. Moreover, human introduction could not account for the great range of fusconaiads in the southern Atlantic drainage as represented by Johnson (1970: 301-302), some of whose records of *"Pleurobema" masoni* include *Fusconaia*, as well as *Lexingtonia*. (5) As noted above, *F. masoni* is not an atavistic *Lexingtonia*. (6) Although still resurrected from time to time, the notion that overland transport by animals is important in naiad distribution was discredited by van der Schalie (1945).

In view of these considerations, it is clear that penetration of the Atlantic drainage by *Fusconaia* was realized exclusively by dispersal across the Appalachian Mountains on glochidially infected hosts. The assumption that the Tennessee River drainage has contributed directly to the Atlantic drainage naiad fauna does

furnish an explanation of the fact that *Lexingtonia* has been recorded in only these 2 drainages. However, in spite of the slight resemblance of *F. masoni* to *F. barnesiana*, there is no geological evidence that an Atlantic drainage river system has ever captured Tennessee headwaters or that mussels could have entered the Atlantic drainage by subterranean migration of hosts in the Appalachians.

Johnson (1970: 379) called attention to the similarity of *Villosa constricta* (Conrad 1838) of the Atlantic drainage to *V. vanuxemensis* (Lea 1838) of the Tennessee and Cumberland River drainages. This would support a theory of Tennessee and Atlantic drainage intercourse were it not that a close anatomical relationship between these *Villosa* has not been demonstrated and that the genus is represented in the Ohio River drainage (see Ortmann, 1919: 261-270).

A more credible explanation of the known distribution of *Lexingtonia* assumes that the ancestral Mississippi basin fusconaiad stock had already differentiated in the directions of modern genera by the early Pleistocene, when there arose an opportunity to invade the Atlantic drainage as the ancestral Roanoke River system broke through the Appalachians in western Virginia and captured headwaters of the Teays (ancestral New) River, after which the Roanoke suffered piracy by the early James River system (Ross, 1969, gave a detailed chronicle of these events). This opportunity was exploited by precursors of *Fusconaia* and *Lexingtonia*, and the remarkably similar adult shells of modern Atlantic drainage fusconaiads developed as common responses to the unaccustomed rigors of life in the mud and sand floors of the comparatively turbid, sluggish and lime-poor streams of the Piedmont and Coastal Plain. Meanwhile, the ancestors of *Fusconaia* speciated successfully throughout the Mississippi basin and spread to the Gulf drainage. This was accomplished at the expense of the *Lexingtonia*-type, which appears to have died out beyond the Atlantic drainage except for the relict *L. dolabelloides* (Lea 1840) of the Tennessee drainage (see Ortmann, 1921: 83-85).

This account has the added advantage of (1) suggesting why shells of *Lexingtonia dolabelloides* resemble Mississippi basin *Fusconaia* more than fusconaiads of the Atlantic drainage; (2) indicating why *Lexingtonia* has never been detected in the Ohio River drainage; and (3) precluding dissection of Ortmann's concept of *Lexingtonia* on the unwarranted assumption that it embraces convergent organisms of different lineages in the Atlantic and Tennessee drainages.

No other theory so persuasively accounts for the distributions (Johnson, 1970: 301, 379-380) of *Villosa constricta* and another exclusively Atlantic drainage species, *Pleurobema collina* (Conrad 1836). These species must have evolved from ancestors which entered the Atlantic drainage through the Roanoke and James River systems and spread southward — but not so far as the Savannah system, so there is no possibility that they reached the Atlantic drainage from the Apalachicola system.

Lasmigona subviridis (Conrad 1835) is another species whose distribution reflects former confluence of the Atlantic and ancestral upper Ohio River drainages. This species occurs in the New and Greenbrier Rivers of the latter drainage and throughout the Atlantic drainage from the Hudson River system of New York through the Savannah River system, but *Lasmigona* is not represented in the Apalachicola River system (Johnson, 1970: 282, 285, 345-346). *L. subviridis* doubtless originated in the Atlantic drainage, failed to reach the Apalachicola and, as originally proposed by Ortmann (1913: 372), used the Roanoke-Teays confluence for *westward* dispersal.

SUMMARY

Notice is taken of the first fully substantiable records of the freshwater mussel genus *Fusconaia* Simpson 1900 (Mollusca: Bivalvia: Unionacea) in the Atlantic

drainage of eastern North America. Detected in the Cape Fear, Savannah and Ogeechee River systems (i.e., in Georgia and North Carolina), the specimens are identified with *Unio masoni* Conrad 1834 from the Savannah system. The term fusconaiad is introduced and defined. The organism is redescribed under the combination *Fusconaia masoni* (Conrad 1834). Characters of the beak sculpture and reproductive anatomy confirm the generic diagnosis and are required to separate this species from Atlantic drainage populations of the closely related *Lexingtonia* Ortmann 1914. The glochidial host of *F. masoni* is unknown. The difficulties in classifying the fusconaiad genera below the superfamily level are discussed. The legitimacy of a generic concept of *Lexingtonia* is defended. It is proposed that precursors of modern Atlantic drainage *Fusconaia* and *Lexingtonia* migrated from the ancestral New River drainage during its former confluence with the Roanoke River system.

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PSEUDOSKENELLA DEPRESSA GEN. ET SP. NOV., AN ECTOPARASITE ON *GALEOLARIA*

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ABSTRACT

A short-spired pyramidellid, *Pseudoskenella depressa* gen. et sp. nov., is described, which is an ectoparasite on intertidal encrustations of the tubicolous polychaete *Galeolaria caespitosa* (Lamarck) in South Eastern Australia. The new genus differs from all other genera of the family, except *Cyclostremella* Bush, in having a low spire and a simple shell similar to that found in several families of lower prosobranchs.

INTRODUCTION

The family Pyramidellidae contains a large and extremely diverse assemblage of mostly small-sized gastropods, many, if not all, of which feed suctorially on other invertebrates (Robertson & Orr, 1961). The species described below lives together with *"Egila" mayii* (Tate, 1898) on *Galeolaria caespitosa* (Lamarck, 1818), a tubicolous polychaete, the tubes of which form dense masses on the middle and lower shore in New South Wales (Dakin, Bennett & Pope, 1960). Laseron (1951: 299) recorded another pyramidellid, *Odostomia indistincta* (Henn & Brazier, 1894), living on intertidal *Galeolaria* in Port Jackson (Sydney Harbour).

Pseudoskenella gen. nov.

Type species: *Pseudoskenella depressa* sp. nov.

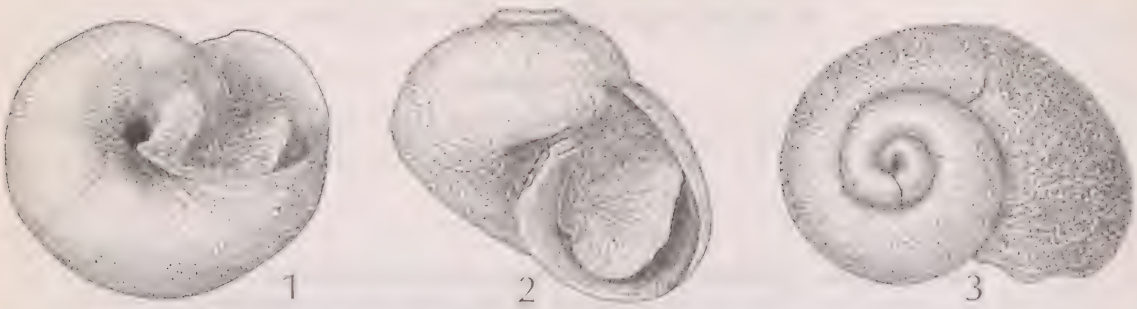
Etymology: *Pseudo* - false (Greek); *Skenella* Martens & Pfeffer, 1886, a genus of the Eatoniellidae which is superficially similar to the new genus (see Ponder, 1965).

Shell: small, thin, umbilicate, smooth, with simple but relatively large aperture and low spire. Protoconch of 1 1/4 whorls, first 1/2 whorl descends slightly, resulting in the apex being partly immersed. Columella concave, smooth, broadly reflected, inner lip a thin glaze on parietal area.

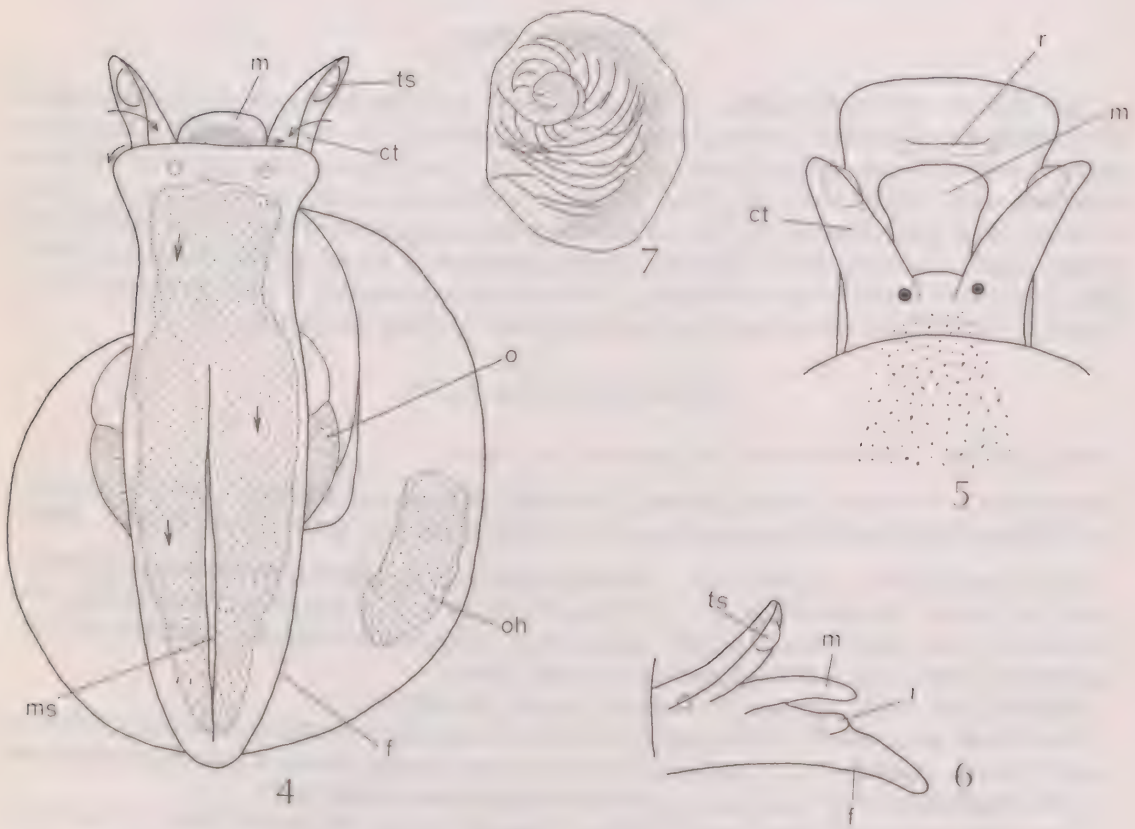
Operculum: thin, simple, the spiral small, indistinct.

Headfoot: with short, elongately triangular cephalic tentacles bearing a bulge on their distal concave face and with eyes at their inner bases, a broad mentum and a well developed foot bearing a posterior pedal mucous groove.

The new genus differs from all other genera in the Pyramidellidae, except *Cyclostremella* Bush (Robertson, 1973), by its low spire. It is also distinctive in its smooth shell, in the lack of a columellar plate and in the protoconch showing only a slight indication of heterostrophy. The features of the headfoot and superficial anatomy are very like those of *Odostomia* species (Fretter & Graham, 1962; Maas, 1965) and because of this and the simple shell features, *Pseudoskenella* is placed in the subfamily Odostominae. *Cyclostremella humilis* Bush, 1897, the type species of *Cyclostremella*, differs from *Pseudoskenella depressa* in having a slightly sunken spire, a wide umbilicus, a differently shaped columella, a distinct posterior apertural sinus, and in being sculptured with fine spiral threads.



FIGS. 1–3. *Pseudoskenella depressa*. Holotype.



FIGS. 4–7. *Pseudoskenella depressa*. FIG. 4. Ventral view of animal. FIG. 5. Lateral view of head and anterior end of foot. FIG. 6. Dorsal view of head. FIG. 7. Operculum. ct, cephalic tentacle; f, foot; m, mentum; ms, pedal mucous gland opening; o, operculum; oh, orange-yellow region of hypobranchial gland; r, transverse ridge; ts, tentacular swelling.

There are, possibly, a few genera in the Cyclostrematidae and in the Vitrinellidae that have some superficial similarity to *Pseudoskenella*. A review of the generic names available has shown that *P. depressa* cannot be assigned to any of them with certainty.

Pseudoskenella depressa sp. nov. (Figs. 1-3)

Shell: small, depressed turbinate, smooth, umbilicate, semi-transparent yellowish-brown to opaque whitish when eroded. Protoconch of 1 1/4 smooth, strongly convex whorls, the first 1/2 whorl deviated inwards and beneath the succeeding whorl. Teleoconch of almost 2, strongly convex whorls. Sculpture of fine growth-lines, sometimes conspicuous, sometimes very weak and sub-obsolete; irregular spiral scratches usually present. Suture distinct, narrowly false margined. Aperture large, outer lip thin, inner lip slightly thickened and expanded as a broad, smooth columellar plate (broken slightly in type) which stands out beyond base and hides part of the umbilicus in front view. Umbilicus broadly open, deep, smooth except for axial growth lines.

Dimensions:	Height	Diameter
	1.05 mm	1.20 mm (holotype)
	0.85 mm	1.06 mm (paratype, Long Reef)

Operculum (Fig. 7): pale yellowish, thin, simple, with a small spiral at anterior end (when retracted, or left side when extended) and prominent growth lines.

Animal (Figs. 4-6): headfoot semi-translucent white except for scattered dark-grey specks dorsally behind the head. Head with short, ciliated, colourless, narrowly triangular cephalic tentacles (ct), triangular in transverse section, the outer face concave and onto which water currents are directed, with eyes at inner bases. A whitish swelling (ts) just below the anterior end of each tentacle protrudes into the concave face. Scattered whitish subepithelial gland cells can also be seen in the tentacles. The cephalic tentacles are normally held almost erect. Mentum (m) broad, rather long, its anterior edge often precedes foot but generally not placed on substratum. Foot (f) well-developed, with a longitudinal, deep, mucous groove (ms) in its posterior half and translucent white, subepithelial mucous glands over most of the sole. A low, transverse ridge (r) lies on the dorsal surface of the propodium. Cilia on the anterior edge of the foot move particles laterally from the centre and those on the sole beat posteriorly, presumably providing most of the locomotory action.

Mantle cavity with a thick, but small, yellowish-orange region of the hypobranchial gland (oh) on the right side. Remainder of hypobranchial gland colorless. Ctenidium absent. The gonad is yellowish in colour and is simultaneously hermaphrodite (as shown by sectioned material). Digestive gland loaded with conspicuous black granules. Proboscis very long and narrow (Fig. 8), 3 times length of shell when fully extended and its surface is minutely pustulose. A sucker-like swelling at its tip is present.

Localities: Boat Harbour reef, north of Cronulla, New South Wales (N.S.W.), 6 Sept. 1971. Coll. W. F. Ponder. On shaded *Galeolaria* clumps, between mid and low tide. Holotype (C. 90981) and many paratypes (C. 90983). East end of Long Reef, Collaroy, N.S.W. 8 Aug. 1971. Coll. W. F. Ponder. On shaded *Galeolaria* just above low tide. Paratypes C. 90980, C. 90982). Same locality, 10 March, 1970, coll. P. H. Colman, 20 specimens, 2 each sent to the following: British Museum, London, England; U.S. National Museum, Smithsonian Institution, Washington, D.C., U.S.A.; Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; National Museum, Wellington, New Zealand; Auckland Museum, Auckland, New Zealand; National Museum of Victoria, Melbourne, Australia; South Australian Museum, Adelaide, Australia; Western Australian Museum, Perth, Australia; Queensland Museum, Brisbane, Australia; and the Tasmanian Museum, Hobart, Tasmania, Australia.

Additional Material Examined. Fairlight, North Harbour, Sydney on *Galeolaria*

FIG. 8. *Galeolaria caespitosa* with *Pseudoskenella depressa in situ*, showing 2 individuals feeding.

(C. 92092) (some specimens also with material collected in this locality near *Galeolaria* under stones (C. 92094) and on short algae (C. 92093)), coll. W. F. Ponder, 23 Dec. 1968; Sandgate, Queensland, pres. C. Hedley, C. 13157; Red Bluff, near Lake Tyers, E. of Lakes Entrance, Victoria, on small rocky, exposed point, washed from medium-sized brown algae, 11 Jan. 1970, coll. W. F. Ponder & P. H. Colman, C. 92095; 4 km N.E. of Beaching Bay, Maria Island, S.E. Tasmania, 42°27.5'S, 148°12'E, in 82 meters, 25 March 1970, coll. W. F. Ponder on F.R.V. "Penghana," C. 92096 (1 dead shell).

It is not known for certain whether the material obtained in habitats other than on *Galeolaria* is due to contamination or whether it is because *Pseudoskenella* has moved from its host searching for a new food supply or, particularly in the case of the dredged material, whether it is living on other tubicolous annelid species.

Notes on Feeding

The host worm is very sensitive to touch and frequently retreats into its tube. *Pseudoskenella* and *Egila mayii* both feed in the same way and frequently (in the laboratory) on the same worms. Both species locate themselves around the aperture of the tube (see Fig. 8) or on the worm's operculum. When the worm has extended its pinnules to feed, the gastropod extends it proboscis, the stylet of which penetrates the epithelium of one of the arms of the pinnules. Because of the extreme sensitivity of the host, feeding is usually intermittent, the ectoparasite being continually poised for instant withdrawal of its proboscis. The gastropod maintains its position on the host with the mucous secreted by the pedal gland. This secretion can be formed into a strong thread along which the animal can climb. Like most small gastropods *Pseudoskenella* can also swim along the surface film (as shown in Fig. 4).

Habitat

The *Galeolaria* masses on which *Egila* and *Pseudoskenella* were found were shaded clumps growing beneath overhanging ledges of rock. Neither species was

found on *Galeolaria* directly exposed to the sun.

Similarity to other species

No other species described as a pyramidellid resembles the new species. There are, however, very great superficial similarities with species placed in families such as the Vitrinellidae, Cyclostrematidae and Orbitestellidae, as well as with *Skenella* in the Eatoniellidae. The most similar species in New South Wales are *Microdiscula pellucida* Laseron, 1951 (= *M. fragilis* Laseron, 1954) and *Lissotesta arenosa* Laseron, 1954. Both species have the apex of the protoconch tilted downwards. The operculum of *L. arenosa* is spiral with a central nucleus and the shell is more globose and the inner lip narrower than in *Pseudoskenella depressa*. *M. pellucida* has a larger, flatter shell than *P. depressa* and a similar aperture to that of *L. arenosa*, to which it is probably related. The generic position of these cyclostrematid species is not certain, but both would be better assigned to *Lissotesta* rather than *Microdiscula*.

ACKNOWLEDGEMENTS

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FECAL PELLETS OF *BIOMPHALARIA GLABRATA*

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ABSTRACT

Spindle-shaped pellets, formed in the cecum of *Biomphalaria glabrata* and other planorbid snails, and consisting of concentrations of microorganisms encased in a membrane, are egested with the feces. An expanded glandular region occurs in the intestine of these snails, comparable in location and gross appearance, but not in function, to the "pellet compressor" described in some other mollusks.

Spindle-shaped pellets typically occur in the feces of freshwater pulmonate mollusks. In a detailed study of the digestive system of *Lymnaea stagnalis appressa* Say, Carriker (1946) described the formation of fecal pellets in an expanded region of the intestine referred to as the "pellet compressor." In studies on *Biomphalaria glabrata* (Say) and other planorbid mollusks, formation of fecal pellets has been observed to occur in the pyloric cecum. An expanded region of the intestine, considered to be homologous to the "pellet compressor," occurs in *B. glabrata* and other planorbidae. This report deals with the structure of the pellets, cecum, and expanded intestinal region in *B. glabrata*, and their relation to each other.

MATERIALS AND METHODS

Observations have been made on intact live snails, fresh aqueous mounts of snail feces, fresh mounts in snail hemolymph of dissections to show the digestive tract, and serial sections of snails fixed in Bouin's solution and stained with hematoxylin and azure-eosin.

RESULTS

Fecal Pellets

The spindle-shaped pellets in the feces of *Biomphalaria glabrata* were found to consist of concentrated masses of microorganisms enclosed in a transparent envelope. The pellets were interspersed with the heterogeneous remainder of the fecal material (Figs. 1, 2, 6, 7). The pellet contents varied according to the microorganisms present in the various snail containers and ingested by the snails; usually either bacteria or green algae. The same organisms occurred in lesser concentrations mixed in with the fecal waste material. In many stained sections or fresh preparations examined under the microscope, pellets contained bacteria appearing morphologically similar in any one snail, but varying in the morphology in snails from different culture containers. Pellets illustrated (except Fig. 4) consisted largely of a single species of spiral, unicellular green algae occurring in many of our snail cultures. In snails from some cultures, however, pellets have consisted of other green algae.

Pyloric Cecum

The pyloric cecum is a blind sac opening into the prointestine near the pyloric end of the stomach (Fig. 3, 4). It is lined by a ciliated epithelium. The opening

of the digestive gland to the prointestine is opposite this pocket. The cecum has internal longitudinal folds forming grooves such that incoming material from the stomach is separated from the outgoing formed pellets that pass to the prointestine (Fig. 5). In the cecum certain microorganisms are concentrated into spindle-shaped pellets, and confining envelopes are formed around them.

Prointestine

The prointestine is lined by a layer of low ciliated columnar epithelium and relatively few secretory cells, except in the typhlosole (Fig. 3, 8, 9).

Glandular Intestine

The expanded region of the intestine, homologous to the "pellet compressor" (Carriker, 1946), appears histologically much like the "midintestine" as described in *Marisa cornuarietis* by Lutfy & Demian (1967) and by Demian & Michelson (1971). This region of the intestine consists of part of the anterior curve after passing through the loop of the anterior aorta (Fig. 3) (Richards, 1973). It lies adjacent to or becomes embedded in the albumen gland. A typhlosole is present in the glandular intestine. The epithelial cells of the glandular intestine are greatly elongated, this being the cause of the increased diameter of the intestine in this region (Fig. 10, 11, 12). The surrounding layer of muscle and connective tissue is no thicker than in other parts of the intestine. The epithelium appears to consist primarily of 2 types of cells: the ciliated columnar cells, wider at the ciliated end and tapering to a narrow base, with elongate nuclei mostly distal to the middle of the cells and with scattered chromatin granules; and secretory cells with broad middle and basal portions and tapering toward the distal or lumen end, with nearly spherical nuclei located in the middle or basal parts of the cells and with compact central masses of chromatin. When Pan (1958) observed "it is likely that the prointestine is a secretory zone," this probably included the region described above.

DISCUSSION

The term "fecal pellet" has been applied to 2 different types of egested objects in mollusks. In some mollusks, apparently the entire fecal "rod" is compressed into successive "pellets." This is described by Lutfy & Demian (1967) as occurring in the mid-intestine in *Marisa*. The formation of fecal pellets in an expanded region of the intestine, referred to as the "pellet compressor," was described for the pulmonate snail *Lymnaea stagnalis appressa* by Carriker (1946). This expanded region of the intestine has also been referred to as the "pellet compressor" in other pulmonate snails by other authors. In *Biomphalaria glabrata* and all other Planorbidae we have studied, spindle-shaped pellets are interspersed in the fecal string, but the main bulk of the fecal material is not egested in the form of pellets. The pellets contain concentrations of microorganisms enclosed in a thin transparent envelope.

All figures (Figs. 1–12) are of *Biomphalaria glabrata*; all sections are stained with hematoxylin and azure-eosin.

FIG. 1. Fecal string with included fecal pellets, 25X. FIG. 2. Fecal pellet in feces showing pellet envelope (E), 100X. FIG. 3. Fresh dissection of juvenile snail showing stomach (S), pocket (K), cecum with forming pellet (C), junction of digestive gland with prointestine (J), pellet in prointestine (P), heart (H), glandular intestine (G), intestinal loop (with pellets) associated with digestive gland (D), 12X. FIG. 4. Section through stomach wall (S), pocket with ciliated epithelial folds (K), cecum containing forming pellets (C), 100X, scale line = 50μ.

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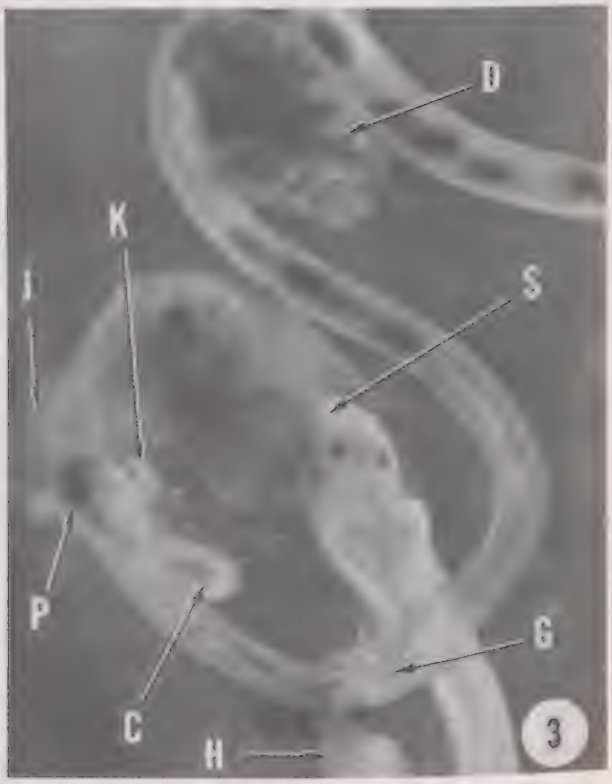
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Formation of these pellets in the Planorbidae occurs in the cecum, apparently following the filtering out of the microorganisms from ingested material by a pocket with ciliated folds, located at the pyloric end of the stomach.

An expanded region occurs in the intestine of Planorbidae, considered homologous to the "pellet compressor," and referred to here as the glandular intestine. It was termed a "glandular stomach" by Marcuzzi (1950). This region has an epithelium consisting of greatly elongated cells, with many secretory cells interspersed with the ciliated columnar cells. The muscle layer around this region of the intestine is poorly developed. Richards & Merritt (1967) found this region of the intestine to be the primary site of entry to the hemocoel of first stage larvae of *Angiostrongylus cantonensis* ingested in feces from infected rats.

The occurrence of these pellets raises interesting questions as to how and why the microorganisms are thus concentrated and the nature of the envelope enclosing them.

CONCLUSIONS

In *Biomphalaria glabrata* the feces are egested as a rather uniform string of heterogeneous material interspersed with spindle-shaped pellets consisting of concentrations of microorganisms encased in a membrane. These pellets are formed in the cecum.

An expanded region occurs in the intestine, comparable in location and gross appearance to the "pellet compressor" described in some other mollusks. In *Biomphalaria glabrata* this is a glandular region.

ACKNOWLEDGEMENTS

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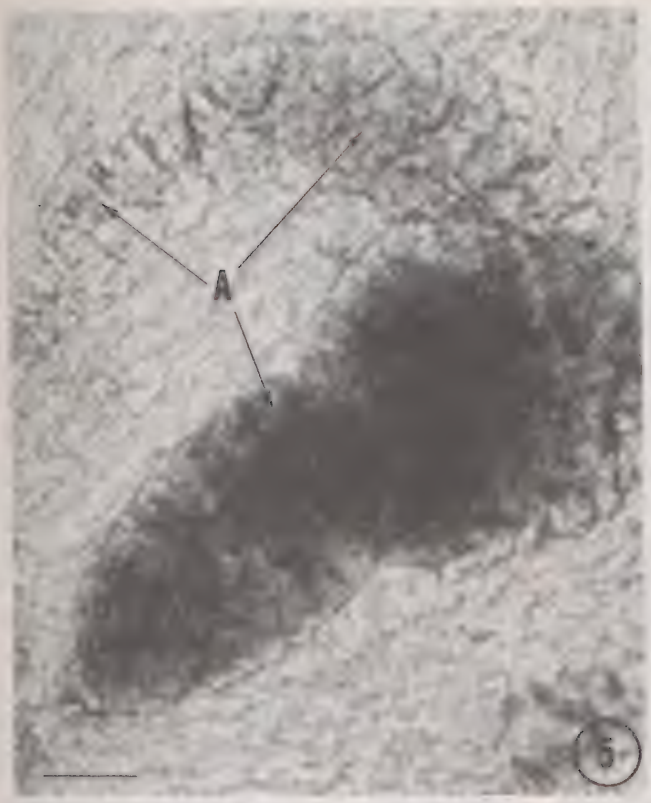
FIG. 5. Fresh preparation of cecum showing pellet of unicellular green algae (A): 100X, scale line = 50μ. FIG. 6. Longitudinal section of rectum showing heterogeneous fecal material and pellets containing algae (A), 100X, scale line = 50μ. FIG. 7. Section of rectum showing rectal fold (R), fecal material (F), and fecal pellet with algae (A) and surrounding envelope, 400X, scale line = 10μ. FIG. 8. Section of typhlosole of prointestine showing ciliated columnar cells (C = cilia) with elongate medial nuclei and secretory cells with small spherical basal nuclei, 400X, scale line = 10μ.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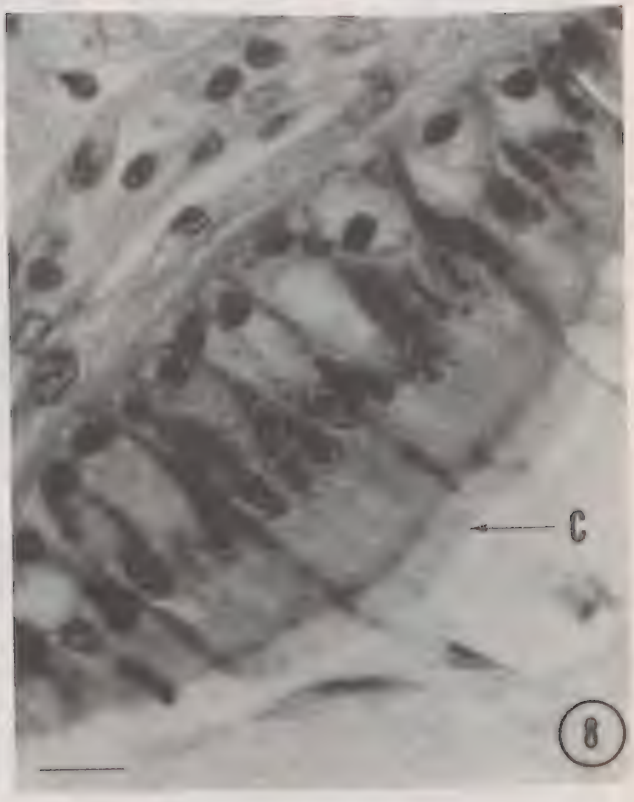
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FIG. 9. Section of epithelium of prointestine with low ciliated columnar cells (L = lumen), 400X, scale line = 10μ. FIGS. 10, 11, 12. Sections of wall of glandular intestine showing long ciliated columnar cells (C), mucus secreting cells (S), and thin muscle and connective tissue covering, (L = lumen), 400X, scale line = 10μ.

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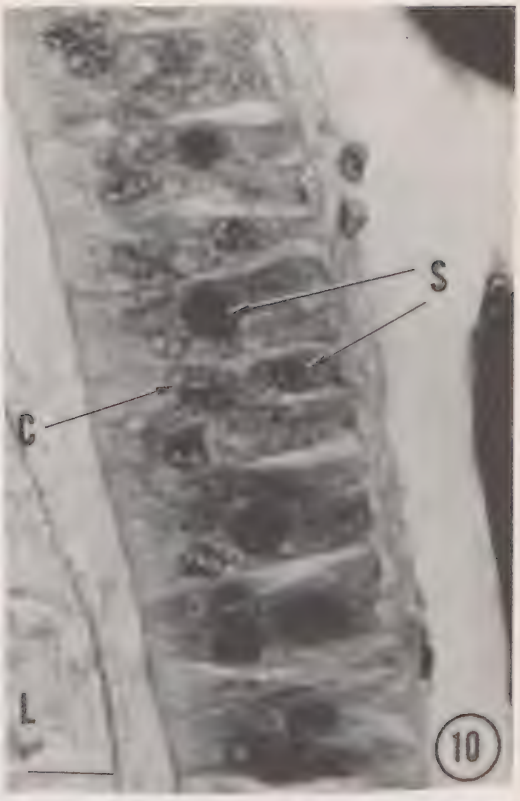
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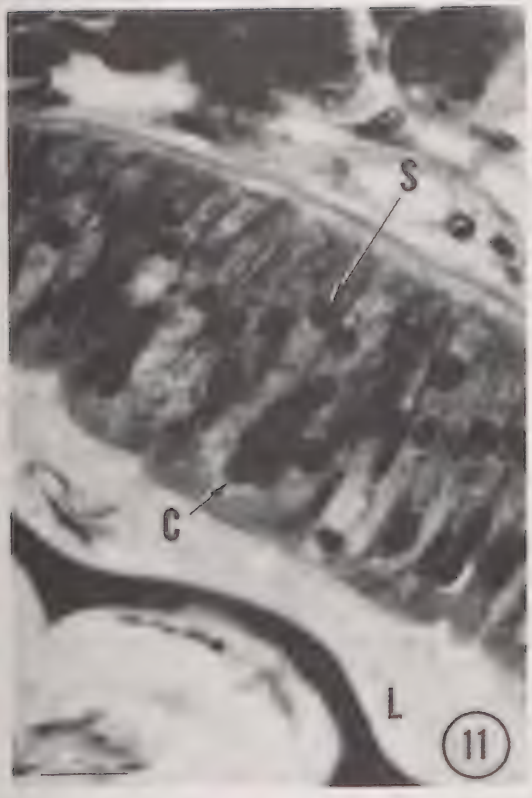
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Malacological Review, 1973, 6: 133-138

INHERITED VARIABILITY IN THE COURSE OF THE INTESTINE IN *BIOMPHALARIA GLABRATA*

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ABSTRACT

Variability in the course of the intestine was observed in *Biomphalaria glabrata*. In some snails the intestine is shortened, with omission of the loop normally associated with the digestive gland. This condition is inherited and genetic stocks have been derived by selection in which the shortened intestine occurs in high frequency. When such snails are infected with *Schistosoma mansoni*, some secondary sporocysts commonly develop on the intestine free of the digestive gland, a situation which may be of value in experimental studies of the parasite.

Variability in the course of the intestine has been observed in *Biomphalaria glabrata* and several other planorbid mollusks studied. Selection for various modifications of intestinal morphology has been followed through several generations to test for inheritance.

MATERIALS AND METHODS

Genetic studies of these variations have involved stocks of *Biomphalaria glabrata* from different geographic origins, particularly lines derived from crosses between Brazilian and Puerto Rican snails (NIH-MII) using methods previously described (Richards, 1970, 1973c; Richards & Merritt, 1972).

RESULTS

Normal intestine

The proximal loop of the intestine of *Biomphalaria glabrata* normally proceeds from the posterior end of the stomach anteriad along the right side of the stomach, passes transversely in close association with the heart (including an expanded "glandular intestine" region, Richards, 1973b) and then posteriad on the left side of the stomach. Continuing as the "ascending intestine" it forms a loop embedded in the digestive gland, to return anteriad as the "descending intestine" to the left of and ventral to the stomach (Figs. 1, 5; see also Basch, 1969).

Right ascending intestine

It has been observed that in several stocks of *Biomphalaria glabrata* the intestine does not always loop around the stomach. Not infrequently the ascending intestine doubles back on the right side of the stomach (Fig. 6). Although this morphological variation, which results in displacement of the stomach to the left side, appears to occur more frequently in some snail stocks than others, it has not been observed in high frequency and selection for the character has so far failed to result in noticeable increase in frequency.

Coiled intestine

Elongation of the intestine, resulting in coiling of the intestine in the area between stomach and heart, has been observed frequently in several stocks of *Biomphalaria glabrata* (Fig. 2). As with the previous character, selection has failed to produce observed increase in frequencies of this intestinal modification.

Short intestine

Another observed modification of intestinal morphology consists of shortening of the intestine, involving particularly the loop that is normally embedded in, and intimately associated with the digestive gland. In some snails this loop is reduced, and in extreme cases of intestinal reduction the digestive gland is by-passed except for its connection to the prointestine (Figs. 3, 7). In most populations of *Biomphalaria glabrata*, this condition is observed in less than 1% of the individuals, if at all. Selection for this morphological character has resulted in several stocks of *B. glabrata* showing high, though variable, frequencies of short intestine. One of our genetic stocks, identified as NIH-MH-c^bc^b-126 (Richards, 1973c) and maintained as a test stock juvenile and adult susceptible to a strain of *Schistosoma mansoni* from Puerto Rico but refractory to a strain from St. Lucia, serves as an example. In this black-eye clonal stock, derived from a single snail after several generations of selection for short intestine, the observed frequencies of short intestine by-passing the digestive gland, through several subsequent generations of selfing were as follows: F_1 generation 25/109 (23%), F_2 generation 62/166 (37%), F_3 generation 47/198 (24%), F_4 generation 41/123 (33%). After several additional generations this stock continues to show frequencies of short intestine similar to those above. If snails showing intermediate degrees of shortening of the intestine were included, the above frequencies would be approximately doubled. The range in degree of shortening of the loop through the digestive gland and the fact that in some cases several generations of selection were required to obtain relatively high frequencies suggest multifactorial inheritance and probably incomplete penetrance.

Circulatory system

The variations in the course of the intestine described above would be expected to be accompanied by variations in the arrangement and size of the related arteries (Basch, 1969; Pan, 1971). As shown diagramatically in Fig. 8, a branch of the albumen gland artery normally supplies at least part of the proximal loop of the intestine, branches of the posterior aorta supply the ascending intestine, and a branch of the cecal axis supplies part of the descending intestine. In the present study observations of the major arteries were made in vivo or on freshly dissected snails. In albino *Biomphalaria glabrata* or blackeye or wild type stock selected for minimal black pigment, the major blood vessels can be observed in intact live snails. Large pigment cells (Richards, 1973a) with pigment ranging from pale strawcolored through bright red to dark brown typically occur attached to the main arteries. In snails in which these pigment cells are red or brown the cells outline the vessels, fascilitating in vivo observations. In snails with both the prointestine and the ascending intestine on the right side of the stomach (Fig. 6), the loop of the anterior aorta was pulled posteriad. In snails with the shortened intestine by-passing the digestive gland (Fig. 7), the main posterior aorta still progressed over the stomach and prointestine to the digestive gland, apparently

FIG. 1. *Biomphalaria glabrata*, left side; normal course of intestine with loop associated with digestive gland, 6X, (I = intestine). FIG. 2. *B. glabrata*, left side; intestine by-passing digestive gland, but long and coiled, 6X. (I = intestine, T = tentacle). FIG. 3. *B. glabrata*, left side; shortened intestine by-passing digestive gland, 6X. (I = intestine, A = albumen gland, S = stomach, D = digestive gland). FIG. 4. *B. glabrata*, piece of intestine removed with intact attached daughter sporocyst. Cercariae were emerging from sporocyst while photomicrograph was being taken, 12X.

I
1

T
I
2

S
A
I
D
3

4

having no association with the remainder of the intestine. A prominent artery, less conspicuous in normal snails and presumed to be the albumen gland artery, branched off the common aorta, passing in close association with the transverse section of the intestine.

Infections with *Schistosoma mansoni*

In *Biomphalaria glabrata* infected with *Schistosoma mansoni*, the daughter sporocysts usually develop in such intimate association with the digestive gland that it is difficult to delineate the extent of a single sporocyst in vivo, or to dissect out an intact daughter sporocyst. Daughter sporocysts are sometimes observed developing on the intestinal wall (Fig. 4), and this appears to occur more frequently in some snail stocks than others. The frequency of *S. mansoni* development on the intestine is high in some of the stocks with a shortened intestine.

DISCUSSION

By-passing of the digestive gland by the intestine in some *Biomphalaria glabrata* and some other species of *Biomphalaria*, *Gyraulus* and *Drepanotrema* appears to have no effect on the physiology of these snails. This suggests that the loop more commonly embedded in the digestive gland may primarily serve the function of lengthening the intestine, the intimate relation to the digestive gland being unnecessary.

When the intestinal loop through the digestive gland is omitted, the artery still in position to serve the intestine beyond the prointestine appears to be the albumen gland artery. Development of daughter sporocysts of *Schistosoma mansoni* on the intestinal wall in a snail with intestine by-passing the digestive gland provides a situation of experimental interest. Development of individual sporocysts and emergence of cercariae from the sporocysts can be observed in vivo and intact sporocysts can be dissected out if desired without involvement of the digestive gland. The higher frequency of daughter sporocysts developing on the intestine in snails with the shortened intestine may be the result of changes in the arteries. Migrating daughter sporocysts were observed actively moving through the small hemolymph sinuses until they reached the large veins along the kidney (Richards & Merritt, 1972). Here they were rapidly swept by the hemolymph current to and through the heart. Leaving the heart, most of the daughter sporocysts could be expected to be carried via the large posterior aorta to the digestive gland. With the increased size of the artery associated with the shortened intestine, presumed to be the albumen gland artery and branching off the common aorta before the posterior aorta, more daughter sporocysts than usual might be expected to enter this artery to develop on the surface of the intestine.

Selection through several generations resulted in relatively high frequencies of shortened intestine maintained thereafter in several stocks of *Biomphalaria glabrata*. It is concluded that this character is determined by multifactorial inheritance.

ACKNOWLEDGEMENT

The technical assistance of James W. Merritt is gratefully acknowledged.

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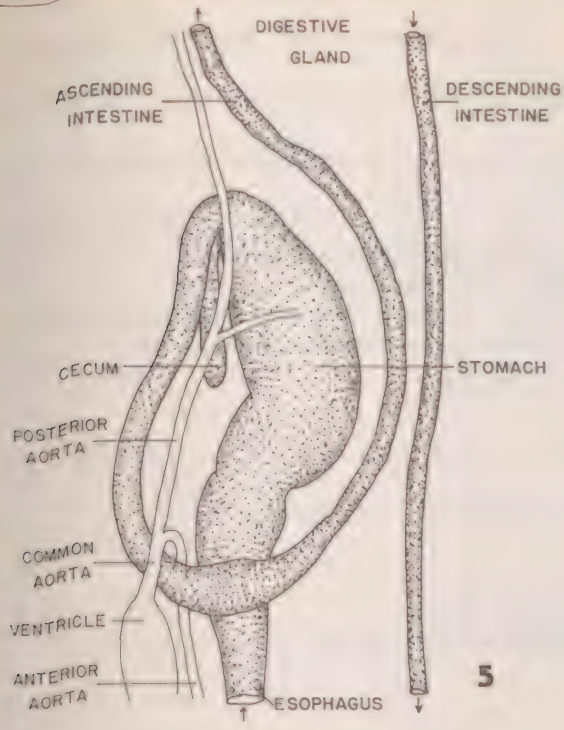

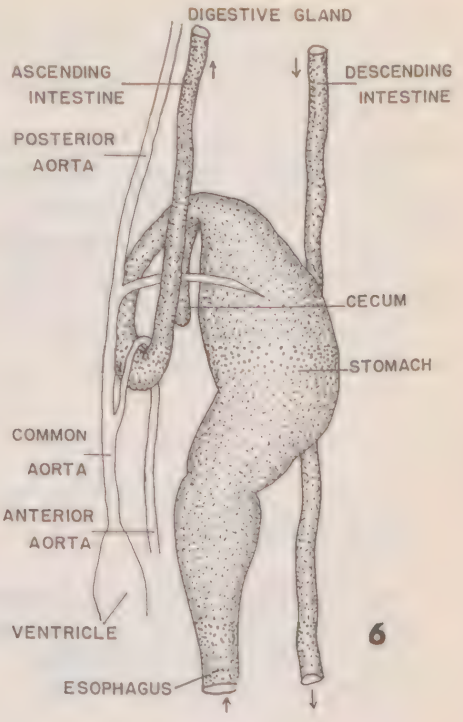

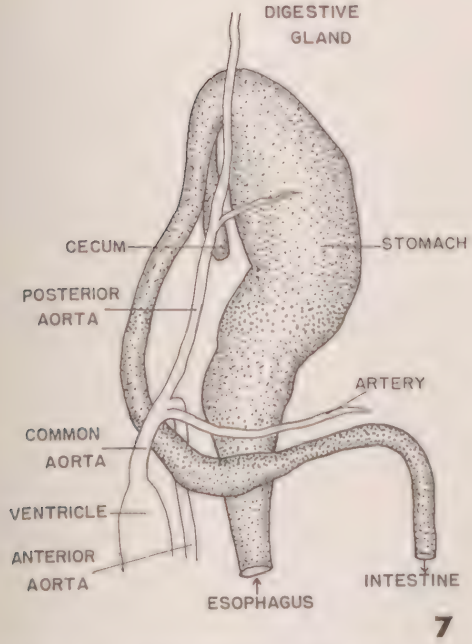

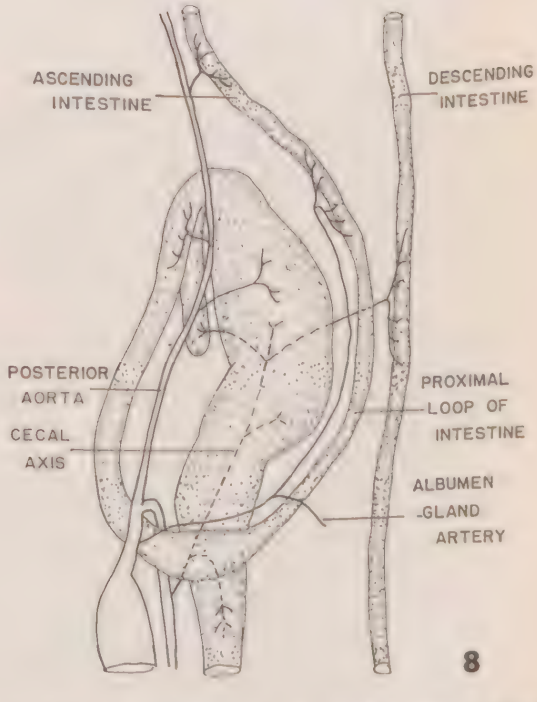

FIG. 5. Drawing illustrating normal course of intestine in *Biomphalaria glabrata*. FIG. 6. Drawing illustrating ascending intestine looping back on same side as prointestine, and related morphology in *B. glabrata*. FIG. 7. Drawing illustrating shortened intestine by-passing digestive gland, and related morphology in *B. glabrata*. FIG. 8. Semi-diagrammatic representation of arterial supply to digestive system of *B. glabrata* (based on Basch, 1969; Pan, 1971; and original observations).

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American Malacological Union

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Convener

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CYTOGENETICS OF GASTROPOD MOLLUSKS

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Cytogenetic studies of gastropod mollusks have been concerned with hybridity, polyploidy, chromosome morphology, supernumerary and sex chromosomes.

Hybridity

Staiger (1954) conducted cytogenetic studies of the muricid snail, *Purpura* (=*Thais*) *lapillus*. In hybrid populations between n=13 and n=18 forms, individuals were found in which, during meiosis, 5 metacentric chromosomes were paired with 10 acrocentrics. The arms of the 10 acrocentric chromosomes remained homologous to the 10 arms of the 5 metacentric chromosomes of the 13-chromosome race (Fig. 1). Presumably the 10 acrocentrics arose by splitting of the centromeres of 5 metacentric chromosomes.

Chromosomal features of the 4 nominal species of *Oncomelania* and their hybrids have been reported by Burch (1960; 1964). All specimens studied of each parental population had 17 pairs of chromosomes as did all hybrid F_1 offspring. A comparative examination of late prophase (diakinesis) chromosomes of the various F_1 hybrids revealed no apparent anomalies that did not also occur as prevalently in the parental stocks. Only normal bivalents with 1, 2 or 3 chiasmata were observed and no univalents, trivalents or quadrivalents were present. Furthermore, all segments of each chromosome seemed to pair completely. Considering the cytogenetic information, the ease of hybridization of the various nominal species, the non-reduced viability of the hybrids and the morphological and biochemical similarities of the parental populations, it was concluded that the 4 nominal species, although isolated and widely separated geographically, were in reality only races of 1 species, *O. hupensis*.

Polyploidy

Polyploidy in mollusks has been previously discussed by Burch & Huber (1966). A polyploid condition is evident when there is an exact multiplication of the normal chromosomal complement. The degree of polyploidy is indicated by the number of multiples of the basic haploid chromosome number. There are 2 main types of polyploidy, autopolyploidy and allopolyploidy. Autopolyploidy is the multiplication of 1 basic genome. Allopolyploids have a chromosomal complement composed of 2 or more genomes, each from a different species. The fact that 2 species can cross may imply at least partial homology (homeology) of parental chromosomes. The pattern of association of chromosomes would differ with the species involved in the crosses. Thus, 2 species with no cytologically detectable evidence of homology between genomes would show only bivalent formation while those with cytological evidence of complete genome homology could variously exhibit multivalents or bivalents formed from chromosome members of the group of 4 homologues. Between these 2 extremes would be the forms showing partial homology. The few molluscan polyploids so far discovered all appear to be allopolyploids.

Polyploidy has been reported in the streptoneuran families Hydrobiidae and Thiaridae and in the euthyneuran families Ellobiidae, Ancylidae and Planorbidae.

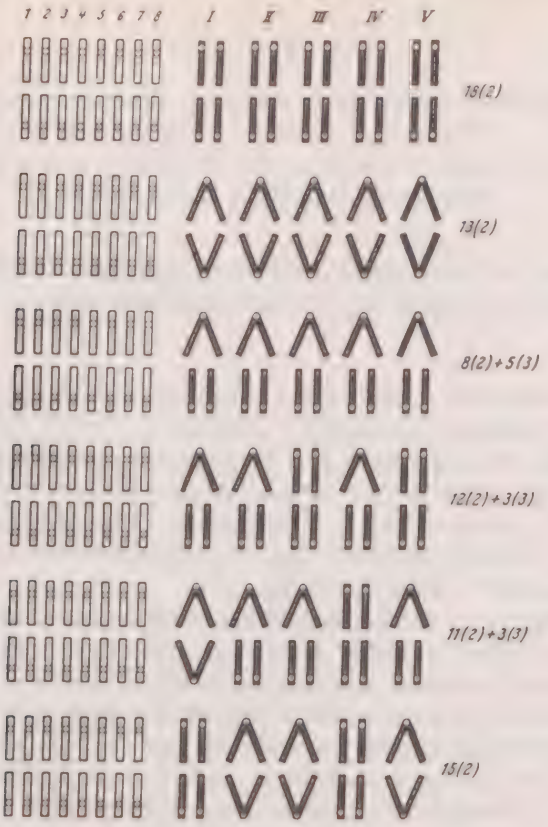


FIG. 1. Chromosomes of hybrid *Purpura* (=*Thais*) *lapillus* (see text) (from Staiger, 1954).

Sanderson (1940) studied the chromosomes of *Potamopyrgus jenkinsi* (Hydrobiidae) collected from Scotland. She found only 1 non-reductional maturation division in the egg and a diploid chromosome number of n=36 in some cells and n=44 in others. Since Rhein (1935) reported the continental race of *P. jenkinsi* to have 20-22 pairs of chromosomes, Sanderson concluded that the British snails were a tetraploid race developed from their diploid parthenogenetic continental relatives.

Melanoides tuberculatus (Thiaridae) is another parthenogenetic species which includes some polyploid populations. Jacob (1959a) studied the chromosomes of 2 "races" which differed in shell characters but occurred together in the same habitat. He found 1 "race" to be diploid (2n=32) and devoid of males, while the other "race" was considered to be polyploid (2n=90-94) and had 3% presumably sterile males. However, it is also possible that he was studying 2 distinct sympatric species. Jacob considered the polyploid race to be an autoallopolyploid which arose from a cross between an autotetraploid parthenogenetic female of 1 species and a diploid male of another species. Because of their high chromosome number, *M. lineatus* (2n=71-73) and *M. scabra* (2n=76-78) were also considered to be polyploid by Jacob.

Another melaniid snail, *Balanocochlis* sp., is also presumably a polyploid judging from its high chromosome number of n=60 (Burch, 1967d).

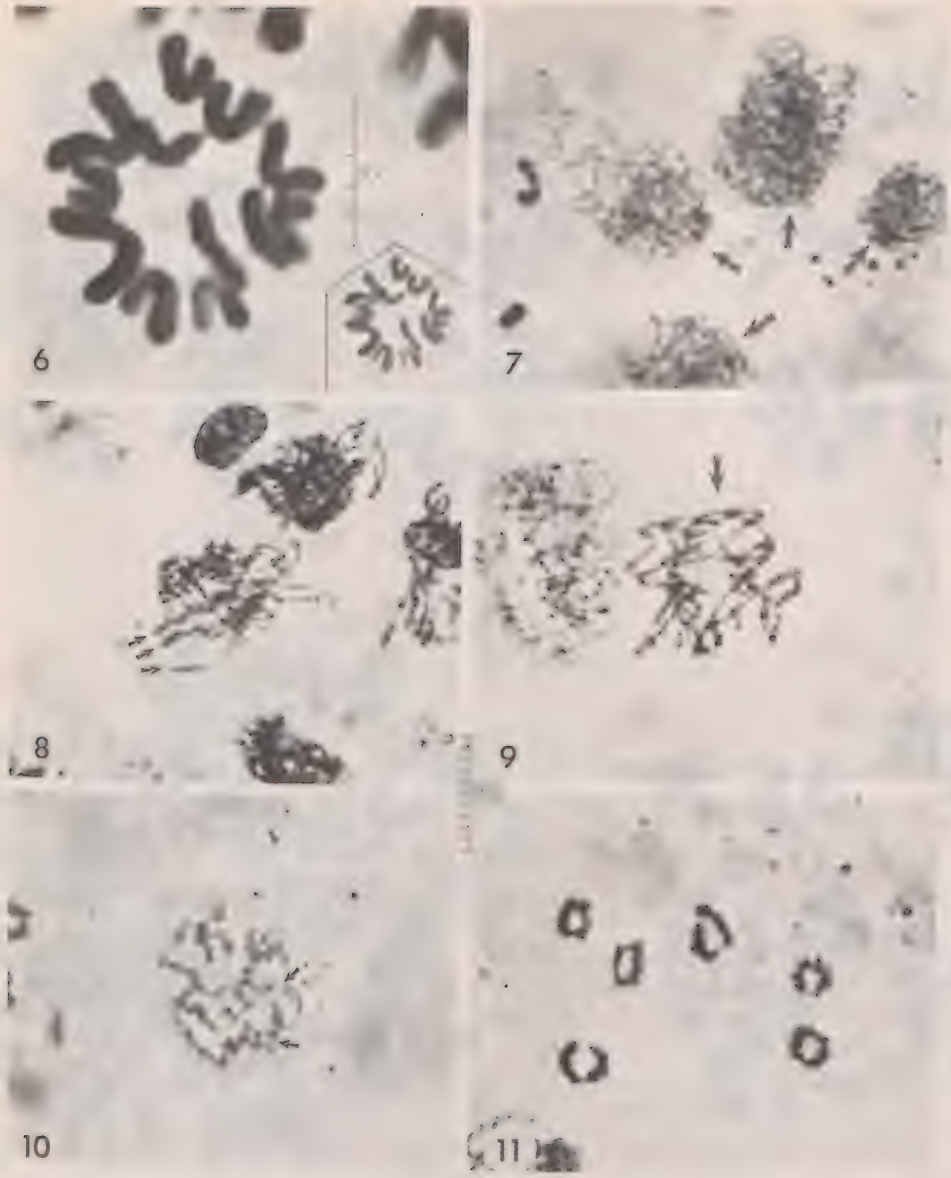
Natarajan & Burch (1966) reported *Melampus coffeus* (Ellobiidae) to have a haploid chromosome number of n=19 and 1 member of a nearby normally diploid but somewhat morphologically different population to have 38 pairs of chromosomes (tetraploidy).

FIGS. 2–5. Mitotic metaphase chromosomes of a polyploid series of *Bulinus* (from Burch, 1964a, 1967b). FIG. 2. *B. ?tropicus*. FIG. 3. *B. truncatus*. FIG. 4. *B. hexaploidus*. FIG. 5. *B. octoploidus*.

Species of the freshwater family Ancylidae have chromosome numbers of n=15, n=30, n=60 and n=17 and 18 (Burch *et al.*, 1960; Burch, 1965a,b). *Rhodacmea cahawbensis* has the chromosome number n=15, while 2 species each of *Ancylus* and *Ferrissia* have chromosomes that are multiples of 15 (n=30 and n=60).

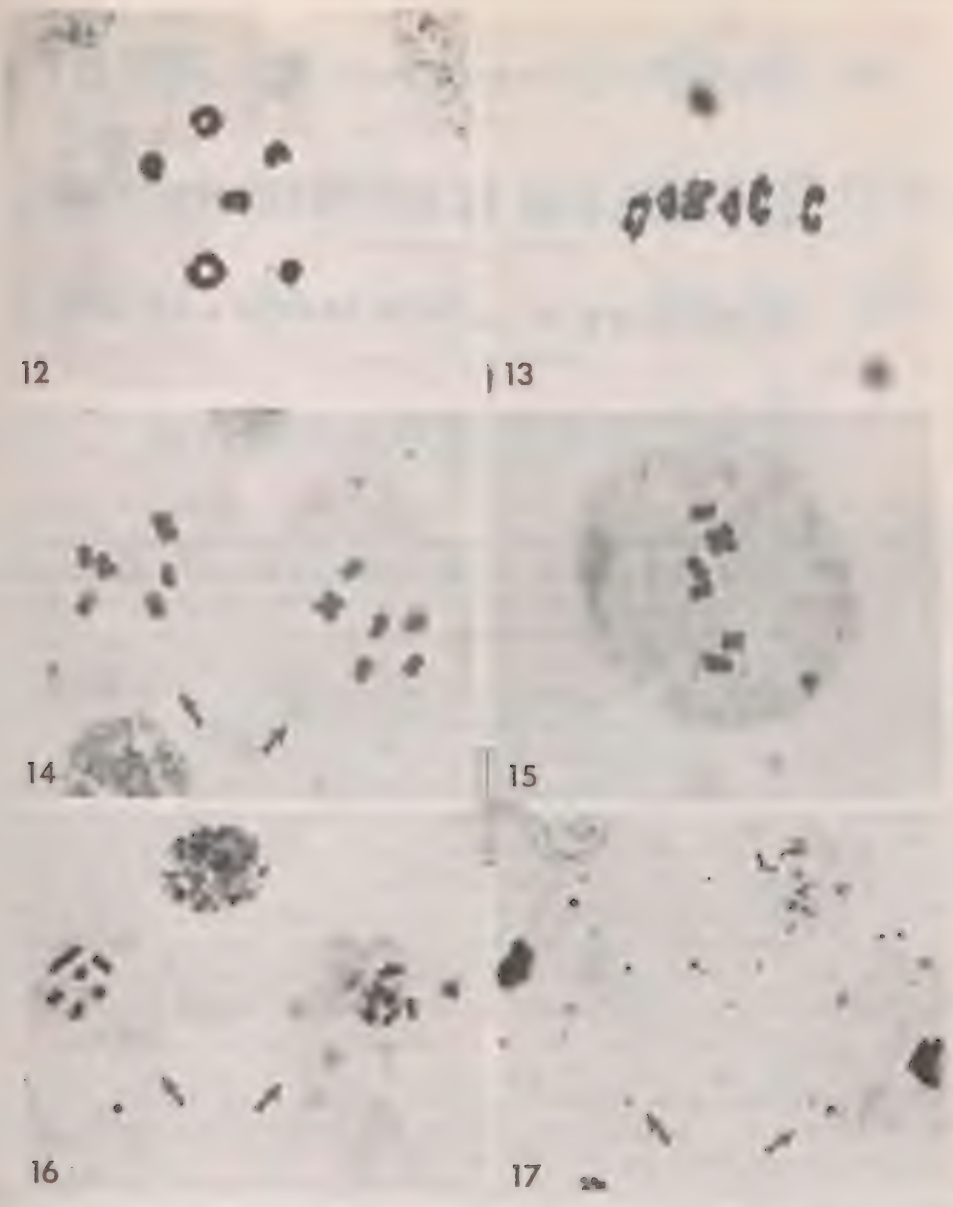
Polyploidy in the family Planorbidae has been reported to occur in representatives of 2 subfamilies. In the Planorbinae, *Gyraulus circumstriatus* has 18 pairs of chromosomes and the closely related tetraploid, *G. parvus*, has 36 pairs of chromosomes (Burch, 1960b; 1965b).

The greatest number of polyploid species discovered so far are members of the planorbid subgenus *Bulinus* (*Isidora*). More than half of the species studied cyto-



FIGS. 6-11. The chromosome cycle in *Catinella vermeta* (from Patterson & Burch, 1966). FIG. 6. Mitotic metaphase. FIG. 7. Leptonema. FIG. 8. Zygonema (arrows point to the paired ends of 6 chromosomes). FIG. 9. Pachynema (bouquet stage). FIG. 10. Early diplonema (arrows indicate places where chromosomes are beginning to "open out"). FIG. 11. Diakinesis.

logically are polyploids (Burch, 1964, 1967a,b; Burch & Lindsay, 1970). As in other planorbid snails, the basic chromosome number in *Bulinus* is n=18. Most of the polyploids are tetraploids (n=36), but hexaploids (n=54) and octoploids (n=72) have also been discovered (Figs. 2,3,4,5). With the exception of 1 population, intermediate chromosome numbers produced by aneuploidy have not been found. Cytologically, these polyploids resemble normal diploids with complete chromosomal pairing during meiosis leading to the contention that they are most likely allopolyploids.



FIGS. 12-17. The chromosome cycle in *Catinella vermeta* (from Patterson & Burch, 1966). FIG. 12. Metaphase I (polar view). FIG. 13. Metaphase-anaphase I (side view). FIG. 14. Prometaphase II dyads in sister cells. FIG. 15. Metaphase II (note spindle fibers). FIG. 16. Telophase II (2 sister cells). FIG. 17. Late Telophase II.

There are no known cases of proven polyploidy in the Stylommatophora. Even though a wide range of chromosome numbers occurs in the Succineidae (n=5-25), intermediate chromosome numbers together with their morphological diversity indicates that the cytological variability is due to aneuploidy.

Chromosome morphology

The morphology of mollusk chromosomes, as seen in the light microscope, is essentially similar to that of other living organisms. The morphological and behavioral aspects of chromosomes during mitotic and meiotic cell divisions have

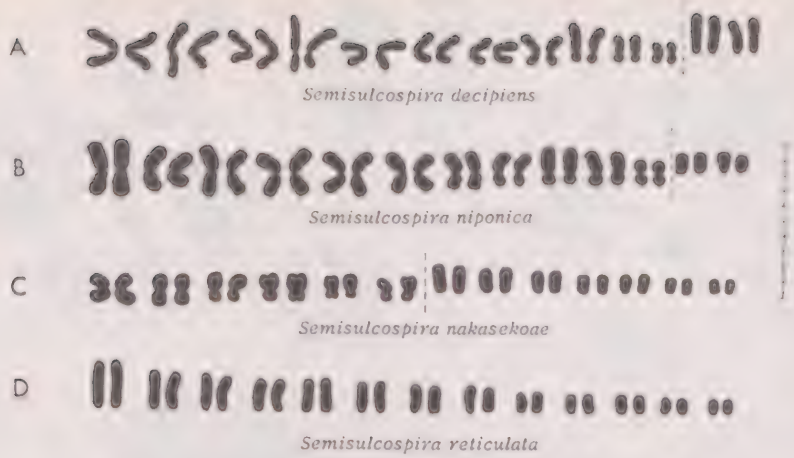


FIG. 18. Mitotic metaphase chromosomes aligned according to shapes and sizes of 4 species of *Semisulcospira* having individuals with 26 chromosomes. Note the proportionate numbers of metacentric and acrocentric chromosomes (separated by the dashed lines) for each species. Measurement line in micra (from Burch, 1967c).

been described in detail for the land snail *Catinella vermeta*, which has only 6 pairs of relatively large chromosomes (Patterson & Burch, 1966). Figs. 6-17 show the chromosomes of *Catinella* in various stages of the chromosome cycle.

With a clearer knowledge of chromosome morphology and behavior, combined with the use of modern techniques of slide preparation and high quality optics, it has been possible to ascertain karyotypes of more than 25 molluscan species. Karyotypes of mollusks have been represented in the usual fashion, by drawings or photographs of homologous chromosome pairs arranged and grouped according to size and centromere position. The karyotype is generally a species specific character and hence is potentially useful in species discrimination. Karyotypes of several species of *Semisulcospira* are shown in Fig. 18 (from Burch, 1967c).

Sex chromosomes

Sex chromosomes have been reported in several species of marine gastropods, 4 freshwater species and 2 amphibious species. Sex-determining mechanisms reported in gastropod mollusks are XX-XY and XX-XO.

Jacob (1959a,b) reported *Melania crenulata* to have a chromosome number of 2n=35 with an XO sex-determining mechanism. The data of these 2 studies, as they concern sex chromosomes, should be verified since the material was prepared by paraffin section technique and the morphology of the chromosomes was somewhat obscure, making accurate karyotype analyses difficult. Jacob also reports *Paludomus tanschaurica* to have a chromosome number of 2n=38 with X and Y sex chromosomes present in males. Jacob designates the largest sex chromosome an X and the smallest a Y, but female individuals were not studied.

Natarajan (1969) reported the presence of a single X chromosome in males of 8 marine and brackish water Indian neritid species. One additional Indian neritid species, *Septaria tessellata*, which exclusively inhabits freshwater has a single X chromosome in males and XX in female individuals.

Burch (1960c) and Patterson (1963) found heteromorphic chromosomes, presumably related to sex determination, in 2 species of *Pomatiopsis*. In *P. cincinnatiensis*, the male chromosome number is 2n=32 (n=16) apparently with a male XY sex

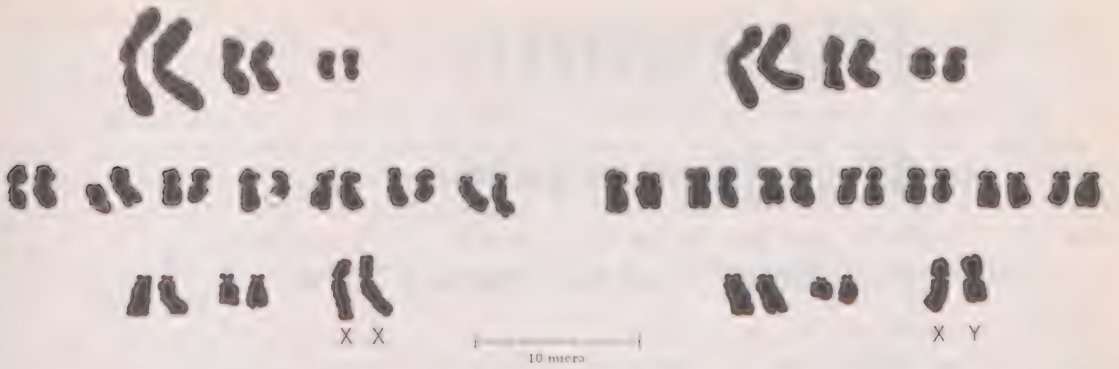


FIG. 19. Karyotype showing mitotic chromosomes of *Tulotoma angulata*, female individual on the left (XX) and male on the right (XY) (from Patterson, 1965).

determining mechanism. In males of *P. cincinnatiensis*, what are considered to be the X and Y elements are the 2 largest chromosomes of the complement. These 2 chromosomes are clearly dimorphic, one being medianly constricted and the other subterminally constricted. Neither has a homologue. In light of this evidence, it was suggested that these 2 elements are dimorphic sex chromosomes. Female members of the species must be investigated cytologically before the X and Y chromosomes can be specifically designated. In *P. lapidaria*, the male chromosome number is 2n=33 (n=17), apparently with a male XO sex determining mechanism. The X chromosome is the largest of the complement; it is subterminally constricted and usually negatively heteropyknotic.

Sex chromosomes in both male and female individuals of the viviparid species, *Tulotoma angulata*, have been observed (Patterson, 1965). The somatic karyotype of *T. angulata* consists of 3 pairs of metacentric chromosomes, 7 pairs of submetacentrics and 2 pairs of almost acrocentric chromosomes (Fig. 19). Two relatively large chromosomes in spermatogonial metaphase cells are dimorphic and do not have similar homologues, as was the case in *P. cincinnatiensis*. One is medianly constricted, the other is distinctly submedianly constricted. In öogonial metaphase cells, the corresponding submedianly constricted chromosome is duplicated and the metacentric chromosome is lacking. This indicates that the submetacentric chromosomes are the X's and the metacentric is a Y chromosome. Therefore, the sex determining mechanism is XX in the female and XY in the males of *T. angulata*.

Supernumerary or Additional chromosomes

Variation in chromosome number among different cells within individuals has been reported to occur in several snail species. Also, variation in chromosome number among individuals of a population has been reported. Supernumerary chromosomes have generally been defined as those which are additional to the karyotype and that are non-homologous or homeologous to chromosomes of the normal complement (White, 1954). Non-homology of extra chromosomes reported to occur in mollusks has not been proven except perhaps in *Helix*. Thus, extra chromosomes reported to occur in mollusks are only provisionally included in the category of supernumeraries. They have been only infrequently observed in mollusks. When present, supernumerary chromosomes may appear in variable frequency among individuals of a population and are not necessarily present in all members. Supernumerary chromosomes have been reported to occur in 1 streptoneuran genus and in 4 euthyneuran genera.

Burch (1967c) found 7 species and subspecies of *Semisulcospira* (*S. niponica*, *S.*

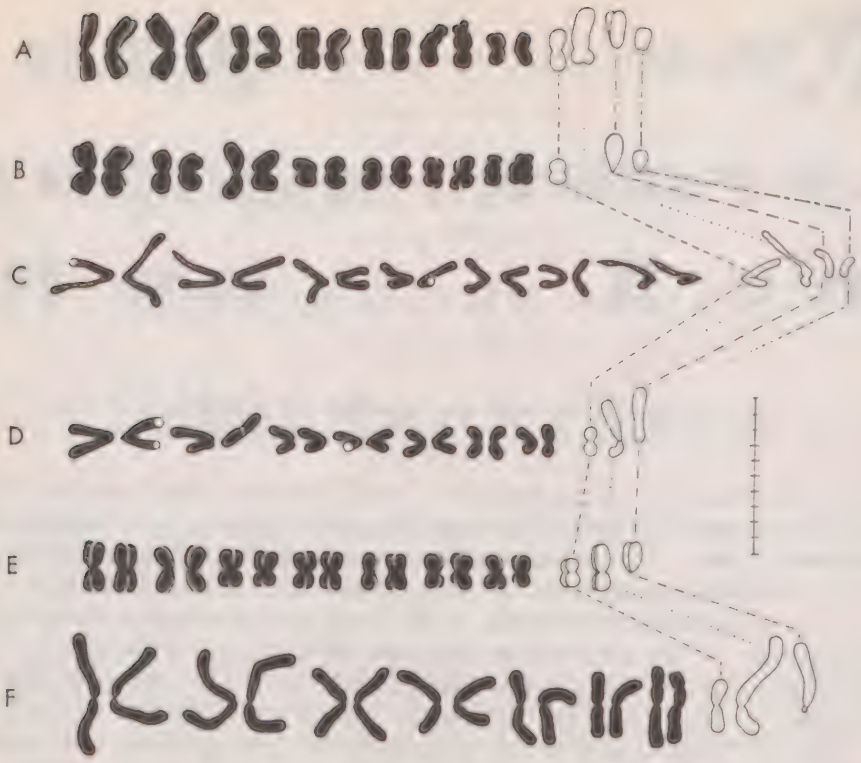
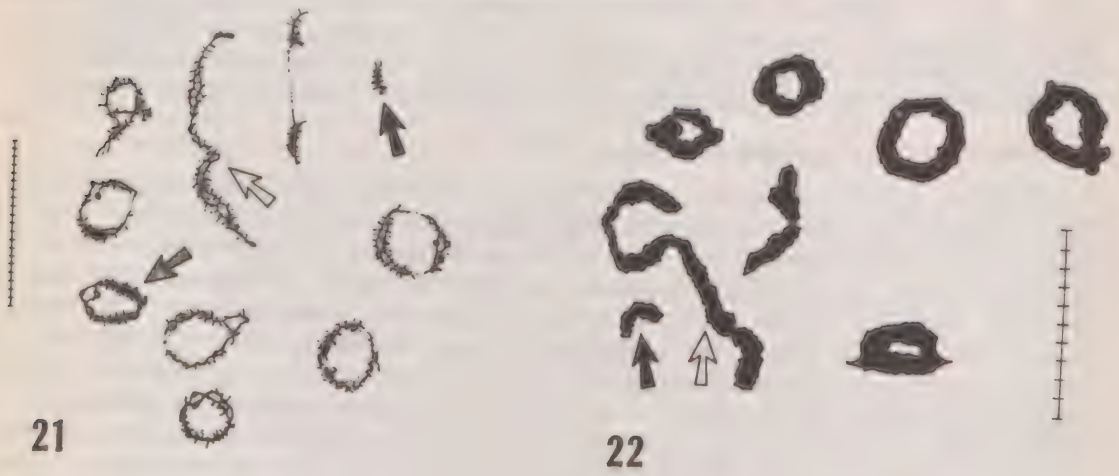


FIG. 20. Gonial prometaphase (F), metaphase (A, B, E) and anaphase (C, D) chromosomes of a female specimen (A-C) and a male (D-F) of *Semisulcospira habei yamaguchi* – Seta River. The 7 regularly occurring chromosomal pairs are placed on the left and shaded. The 3 or 4 odd chromosomes are on the right and are not shaded. The chromosomes were traced from camera lucida drawings and aligned according to shapes and sizes. Measurement line in micra (from Burch, 1967c).



FIGS. 21-22. Meiotic chromosomes of *Semisulcospira habei yamaguchi* (from Burch, 1967c). FIG. 21. Female late diplonema-early diakinesis with 8 bivalents, 1 trivalent (white arrow) and 1 univalent (black arrow). FIG. 22. Male diakinesis with 6 bivalents, 1 quadrivalent (white arrow) and 1 univalent (black arrow).

kurodai, *S. multigranosa*, *S. reticulata*, *S. decipiens*, *S. habei* and *S. h. yamaguchi*) to have extra chromosomes (e.g., Fig. 20), which are most likely supernumerary chromosomes. But, the possibility that they are associated with sex determination cannot definitely be excluded. These extra chromosomes exhibit variable associations in the 1st meiotic division in both female and male individuals. For example, female individuals of *S. habei yamaguchi* had diploid chromosome numbers ranging from 2n=17 to 2n=20 and meiotic cells showed the extra chromosomes to be associated as trivalents and univalents in different individuals (Fig. 21). In male individuals there were similar associations, but with a quadrivalent evident in 1 of them (Fig. 22).

Individuals of 1 population of *Gyraulus deflectus* (normally n=18) were reported by Burch (1960a) to have 3 extra elements which were associated variously as 3 univalents, a univalent and a bivalent or 1 trivalent at diakinesis of the 1st meiotic division. These supernumeraries stained more deeply than the bivalent chromosomes of the complement.

Supernumerary chromosomes were found in 2 populations of *Bulinus natalensis* (Burch, 1964a). The number of additional chromosomes varied from 1 to 3 (n=19-21) among the individuals of 1 population and 1 extra chromosome (n=19) was present in some cells of individuals of the other population. Burch suggested that these varying chromosome numbers may be the result of hybrid origins of the 2 populations.

Husted & Burch (1946) found individuals of *Triodopsis fraudulenta* (normally 2n=58) to have chromosome numbers of 2n=58, 59, 60, 61 (?) or 62 and the bivalents to number 29 or 30 or n=29 with an additional univalent. The authors suggested that the extra chromosomes were perhaps duplications of other chromosomes of the complement. If this should be the case, the chromosomes would be at least partially homologous (homeologous), thereby not qualifying as supernumeraries in the strict sense. Nearly 40% of the specimens of *T. fraudulenta* examined were found to have extra chromosomes. One individual was also found to be mosaic, having cells with 62, 64 and 66 chromosomes (2n). In a footnote to the same paper, Husted & Burch mentioned that some individuals of *Mesomphix oxycoccus* had 29 pairs of chromosomes, while others had 30 pairs.

The most thorough study of supernumerary chromosomes of a mollusk is that of Evans (1960) in which he investigated their occurrence in wild populations of *Helix pomatia*. From 1 to 6 extra chromosomes were found in cells containing the basic diploid complement. All of the extra chromosomes were the same in the 2 populations studied in that they were submedianly constricted and smaller than chromosomes of the basic complement. If only 1 extra chromosome was present it usually did not pair or come to lie on the metaphase plate of the 1st meiotic division, but divided mitotically at the 2nd meiotic division and was always included in daughter nuclei. If 2 additional chromosomes were present, they were usually associated as bivalents in Meiosis I, and more than 2 extra chromosomes appear as univalents or bivalents in the 1st meiotic division. Multivalent associations as have been reported in other gastropods were not observed. Supernumerary bivalents seemed to behave normally during meiosis. Evans felt that the supernumerary chromosomes may have arisen from chromosome change occurring after a period of genotype instability due to inbreeding of these normally cross-fertilizing hermaphrodites. The author also presented a statistical analysis of the frequencies of supernumerary chromosomes between individuals and between primary spermatocytes within individuals. However, this analysis was performed on very small samples of individuals (11 from population F and 14 from K), and will not be discussed further here.

Two other cases of chromosome number variation in the Helicidae are mentioned

by Rainer (1967). He found a population of *Cepaea hortensis* which had a chromosome number of n=30 as compared to n=22 reported by Perrot (1930) for this species. He also found the haploid chromosome number of *C. nemoralis* to vary from n=28 to n=29 in spermatocytes.

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OYSTER GENETICS AND THE PROBABLE FUTURE ROLE OF GENETICS IN AQUACULTURE

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ABSTRACT

Techniques for artificial rearing of commercial edible oysters have already been worked out. The oyster is generally regarded as a prime candidate for intensive aquaculture. Yet to be achieved is the true domestication of the oyster with the development of a variety of different strains so well suited to the methods of intensive culture in hatcheries that a margin of profit is reasonably assured a commercial breeder. Domestication along with some genetic interference with the course of wild populations could further assure that this pelecypod mollusk contributed to the world food supply to the limit of its not insignificant potential. Such "domestication" can be achieved by the deliberate application of genetic methods or, over a longer period, by trial and error breeding. Most likely, it will be accomplished through the combined efforts of researchers and commercial producers, the developments of one opening new avenues of approach to the other. This paper tells what is known already about the genetics of the oyster, reviewing such information in light of its significance in the application of different breeding programs to oysters and to the introduction on natural beds of specially bred new oyster stocks to old wild populations. The review first presents background information on the cytogenetics of oysters, then goes on to consider them in the perspective of inbreeding, selective breeding, intra- and inter-species hybridization, and finally in respect to use in the future of induced mutations in special breeding programs.

Even though the seas are still fished while the land has long been cultivated, farming of the seas has nonetheless been wondered about and experimented with, and on a relatively small scale actually been accomplished. This hope of large-scale farming of the sea now finds expression in technical and scientific undertakings. Aquaculture is one of the main goals of the new Federal Sea Grant Program (Abel, 1971). In December 1971 the Food and Agriculture Organization of the United Nations had its first meeting on "Genetic Selection and the Conservation of Genetic Resources of Fish" and included shellfish in its deliberations (*FAO Fisheries Report No.* 119, 1972).

Techniques for artificial rearing of oysters have been worked out (Loosanoff & Davis, 1963). Shellfish hatcheries open with expectations of much commercial success, but these expectations have yet to be fulfilled (Abel, 1971). Wild oysters can be scarce or almost entirely absent for years, and then become abundant. The commercial oysterman has nowhere near the control over this mollusk that land farmers have over their crops and animals (Sindermann & Rosenfield, 1967; Landers, 1971). Neither has the oyster biologist. This is so even though the oyster is among those marine invertebrates most amenable to artificial culture

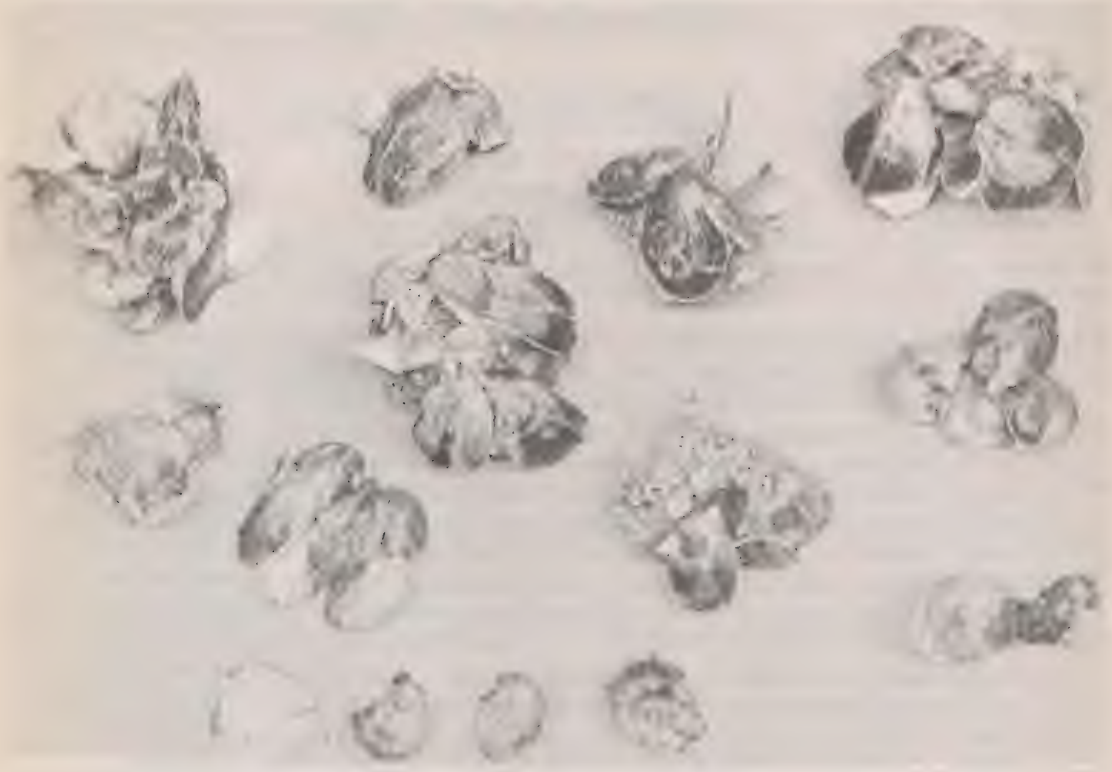


FIG. 1. Wild, about year old set of the commercial American oyster from Long Island Sound. Most are in clumps attached to the old empty oyster shells on which they set.

(Loosanoff & Davis, 1963; Loosanoff, 1972). Certainly, there is more accumulated information on various phases of the biology of oysters than on any other marine invertebrate (Landers, 1971).

An understanding of the genetics of the oyster, along with the establishment of breeds especially adapted to hatchery conditions and to life on new beds in the wild, is one means of gaining additional control. This extra control via genetics and special breeding is probably essential if artificial oyster culture is to become a truly viable industry contributing its full potential to the world's food supply. For discussions of the role of genetics in aquaculture see Cherfas (1969), Longwell & Stiles (1970), Shultz (1970), Longwell (1971), Menzel (1971a, 1971b), Burton (1972), FAO Fisheries Report No. 119 (1972) and Longwell (in press). Work towards genetic control, of course, must go hand in hand with nutritional studies, with studies of molluscan diseases and with the care and preservation of wild stocks. Wild populations are the reservoir of those genes essential to future artificial breeding endeavors.

LIFE CYCLE OF THE COMMERCIAL AMERICAN OYSTER *CRASSOSTREA VIRGINICA*

A thorough study and review of information available for the commercial East Coast American oyster (Fig. 1) was published by Galtsoff (1964). In a recent

FIG. 2. Pelagic larvae of the commercial American oyster near setting. Dark round eyespots are visible in a few.

FIG. 3. Newly set larvae of the commercial American oyster covering the smooth inside of an old oyster shell.

treatise Stenzel (1971) presents a comprehensive study of the distribution, phylogeny and classification of oysters on the basis of their paleontology, anatomy and physiology and ontogeny.

A single, adult female American oyster can spawn as many as 65 million eggs which are fertilized externally. The larvae are pelagic (Fig. 2). At the time they are to metamorphose to the sedentary adult form they develop an eyespot and foot which aid in the setting process whereby the larvae attach themselves to some stationary object (Fig. 2) and begin the sedentary adult phase (Fig. 3). The larvae show a preference for setting on shells of live oysters, or onto empty oyster shells (Figs. 3, 4). Newly metamorphosed larvae are called set or spat.

Conventional electron microscopic and scanning electron microscopic studies have been made of the American oyster male gamete (Figs. 5, 6) and female gamete (Figs. 7, 8) (Daniels *et al.*, 1971, 1973).

CYTOGENETICS

An examination of the male gametogenesis and the spawned and fertilized eggs of *Crassostrea virginica* (Longwell & Stiles, 1968) revealed that its meiotic system,

FIG. 4. Set of the commercial American oyster attached to the inside of an old oyster after a period of growth.

fertilization and early cleavage are of the typical type found in most higher plants and animals (Figs. 9, 10). There are 10 pairs of chromosomes at metaphase I of meiosis of the mature spawned eggs (Longwell *et al.*, 1967) (Fig. 11). Oyster genes are linked together then in 10 different groups. At least in the female, chiasmata in the chromosomes indicate that there is a small amount of crossing-over of the genes making for genetic variability. There is no evidence for any sex chromosomes in this oyster, nor in any of the clams, oysters or mussels yet examined (Ahmed & Sparks, 1967, 1970; Menzel & Menzel, 1965; Menzel, 1968a, 1968b). Absence of sex chromosomes is in keeping with the protandric nature of the American oyster (Galtsoff, 1964).

Crassostrea virginica chromosomes are all short, about the same length, and hardly any of them distinguishable easily from any of the others (Fig. 12, Table 1) (Longwell *et al.*, 1967). The chromosomes of the 2 mussels, *Mytilus edulis* and *M. californianus*, are much longer (Ahmed & Sparks, 1970).

Also studied were the chromosomes of the Japanese oyster, *Crassostrea gigas*, the Puerto Rican oyster, *C. rhizophorae;* the European Flat oyster, *Ostrea edulis;* the United States West Coast Small Olympia oyster, *O. lurida;* and the horse oyster, *O. equestris*. All of these common oysters of both the oviparous and larviparous groups have the same number, size and type of chromosomes as does *C. virginica* (Longwell *et al.*, 1967).

Ahmed & Sparks (1967) and Menzel (1968a, 1968b) have further examined several

TABLE 1. Mean length and arm ratio of early cleavage, colchine-metaphase chromosomes of the American oyster[1,2].

Chromosome number	Mean length in microns	Mean length as percent total length of diploid complement	Mean arm ratio
I - II[3]	3.3 ± 0.18 3.1 ± 0.13	6.4 ± 0.14 5.7 ± 0.07	1.1 ± 0.02 1.2 ± 0.02
III	3.2 ± 0.18	6.1 ± 0.11	1.9 ± 0.20
IV - VI	2.7 ± 0.13 2.5 ± 0.13 2.3 ± 0.08	5.2 ± 0.07 4.8 ± 0.06 4.4 ± 0.08	1.2 ± 0.04 1.2 ± 0.03 1.2 ± 0.07
VII - VIII	2.4 ± 0.10 2.7 ± 0.13	5.2 ± 0.09 4.7 ± 0.06	1.7 ± 0.10 1.9 ± 0.06
IX	2.0 ± 0.10	3.8 ± 0.07	1.3 ± 0.10
X	2.1 ± 0.10	4.0 ± 0.10	2.0 ± 0.03

[1] Published in a manuscript by Longwell *et al.*, *Can. J. Genetics and Cytology*, 9: 845-856, 1967.

[2] Based on 18 early cleavages from 17 different embryos.

[3] One of these two bears a secondary constriction. Therefore, I and II can be distinguished from one another in some cells, but not in all cells measured.

other oyster species, as well as these same ones. They also found no variation in either chromosome number or morphology. Interestingly, in the 4 families of pelecypods studied chromosomally by Menzel, all species and genera within a family had the same number of chromosomes (Menzel, 1968b). However, only relatively few pelecypods have been examined as yet. Now, in view of a recently published treatise on oysters, which places living oysters in more than the old 3 genera and presents a case for a diphyletic family origin of oysters (Stenzel, 1971), other key oyster types ought to be studied chromosomally.

There have been no indications of any chromosome polymorphisms in any of the populations of *Crassostrea virginica* sampled from Long Island Sound. None have been accidentally uncovered in any of the oysters we examined for other purposes that derived from as far north as Prince Edward Island to as far south as Virginia. *C. laperousi* and *C. ariakensis* were reported, however, by a Japanese worker to have 24 chromosomes (2n number) (Kobayashi, 1954). This earlier work based on the older section technique needs confirmation using the newer, better squash technique for chromosome preparation. American malacologists regard *C. laperousi* as a form of the variable *C. gigas* species (Galtsoff, 1964).

Ahmed & Sparks (1970) found some chromosome polymorphisms in the marine mussels, *Mytilus edulis* and *M. californianus*. In the marine gastropod, *Purpura lapillus*, various chromosome forms are associated with a particular distinct habitat. The haploid number is 13 in exposed areas, 18 in sheltered areas, and populations are chromosomally heterogeneous in intermediate habitats (Staiger, 1957).

Chanley (1961) studied the inheritance of variable shell markings in the hard

FIG. 5. Scanning electron micrograph of the sperm of the American oyster. The acrosome is visible in the uppermost sperm head, and mitochondria and the proximal end of the flagellum in the lowermost sperm. X30,000. Courtesy of Dr. E. Daniels, Argonne National Laboratory (from Daniels *et al.*, 1971).

clam, *Venus mercenaria*.

In the intertidal mussels, *Mytilus edulis* and *Modiolus demissus*, there is an allozyme polymorphism which responds to certain physical environmental factors, so that its allelic frequency varies considerably over a relatively short distance (Milkman & Beaty, 1970; Koehn & Mitton, 1972). Battaglia (1970) has reported on non-chromosomal, gene-level polymorphisms in marine copepods that are associated with differences in the environment and ecology.

In contrast to the species, generic and population constancy of the chromosomes of the oysters, the fertilization and early cleavage stages are marked by a high frequency of abnormal variations in chromosome behaviour and number. It appears that this seeming instability also extends to the Japanese oyster, *Crassostrea gigas* (Ahmed & Sparks, 1967), and to the mussel, *Mytilus* (Ahmed & Sparks, 1970). Fertilized and cleaving American oyster eggs from a series of 17 mass-spawned groups with a grand total of 835 spawners had an average of

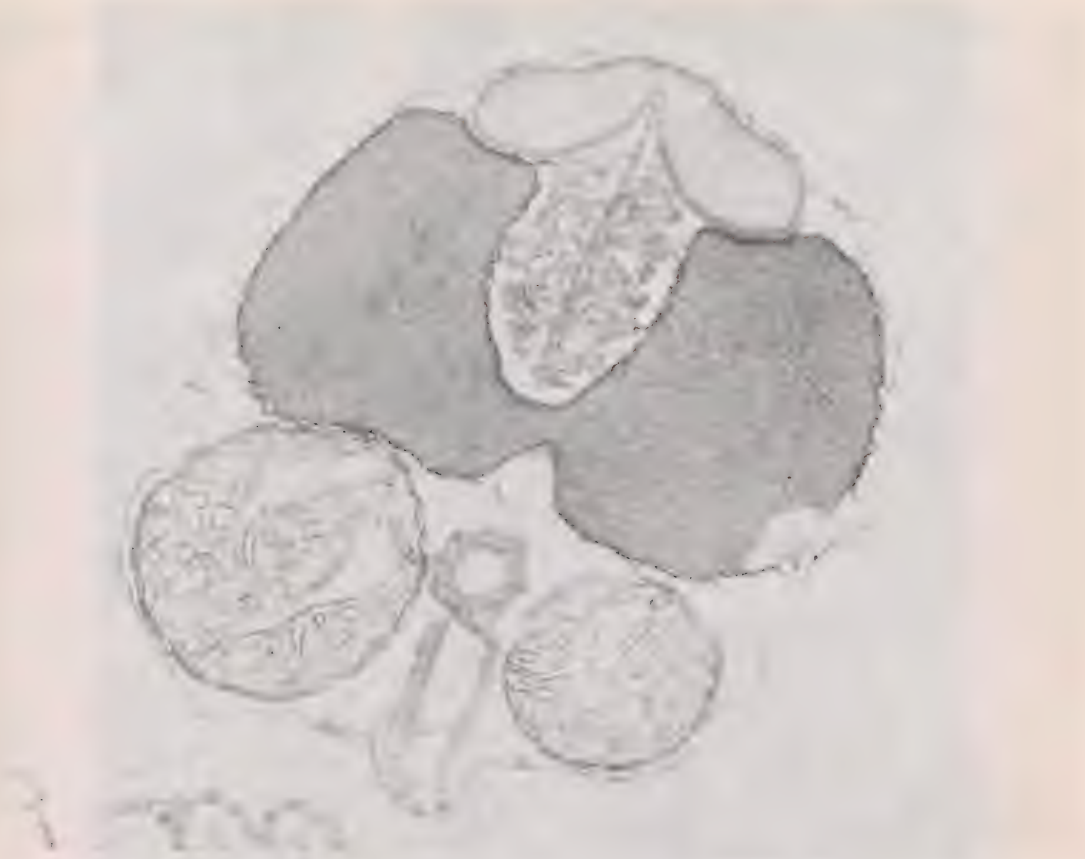


FIG. 6. Longitudinal section through the head and middle piece of the American oyster spermatozoan showing among other finer features from top to bottom the acrosome, nucleus and mitochondria. X44,000. Courtesy of Dr. E. Daniels (from Daniels *et al.*, 1971).

about 30% post-fertilization genetic abnormalities (Table 2). In 13% of the eggs, chromosome numbers were abnormal. This is probably the result of the environmental stresses to which this sensitive, externally fertilized egg is subject (Stiles & Longwell, in press).

INBREEDING

By nature of their life history with a pelagic larval form one might guess correctly that the common oysters have evolved a genetic system depending on outbreeding to maintain vigor even though the adult phase is sedentary. Inbreeding, the converse of this species' natural system of outbreeding, to some extent will accompany mass selection of oysters in commercial hatcheries. More intensive forms of inbreeding could be used to develop special lines for subsequent hybridization, hopefully utilizing the gains of both selection and hybridization, and eliminating the problems of inbreeding in the commercial product.

Full-sib crosses of *Crassostrea virginica* made over a period of a year gave consistently poor development to the first straight-hinge larval stage. A look into this revealed that marked fertilization and early development failures were occurring in these sib-crosses. In 9 cultures an average of as many as 63% of the eggs failed to be fertilized. Only 13% of the out-cross eggs failed to be

FIG. 7. Scanning electron microscope view of the American oyster oocyte surface prior to fertilization. Microvilli are shown throughout the field. X13,500. Courtesy of Dr. E. Daniels, Argonne National Laboratory. (From Daniels *et al.*, 1973).

fertilized. Only 3% of the cleavages in the sib-crossed eggs were normal, as compared to 70% of the cleavages in the out-crosses (Table 3). Some of the inbreeding crosses were characterized by polyspermy when the eggs did get fertilized, and often there was a degeneration of the 1 or more sperm that did penetrate the eggs. Parthenogenesis was increased from an average of 0.5% in the control crosses to 10% in the sib-crosses. Another more extensive series of crosses showed essentially the same crossing difficulties, but with a higher incidence of ineffective fertilization, which probably led to the still greater incidence of parthenogenesis from a control 7% to 29% (Table 4). Prolonged attempts at fertilization resulted in about 20% more of the eggs getting fertilized but this was usually ineffective (Longwell & Stiles, 1972a, in press).

TABLE 2. Chromosome, division and nuclear abnormalities in mass-spawned eggs of the American oyster.

Total percent eggs with abnormalities in 17 different spawning groups[1]	Percent eggs heteroploid	Percent eggs with abnormalities of meiosis	Percent eggs with cleavage and nuclear abnormalities
17	8	8	1
52	16	26	10
28	8	18	4
29	11	14	6
32	10	16	6
34	17	9	8
21	5	14	2
86	43	47	14
11	5	2	4
21	8	8	6
41	21	32	1
18	8	6	4
36	17	12	7
24	18	6	0
16	11	12	0
10	1	5	5
26	7	6	13

[1] Each of the 17 mass-spawned groups had anywhere from 21 to 158 spawners contributing gametes.

An average of 96 eggs were scored cytologically for each of the 17 groups.

Some of the sib-induced parthenogenesis - or at least the tendency to become parthenogenetic enhanced by some other technique as irradiation - might be utilized in special breeding. Absolute pure inbreds might be obtained in this way in 1 as opposed to about 14 generations by the standard procedure. Such inbreds could then be crossed, as in chickens and plants, to produce offspring which show hybrid vigor and still retain the uniformity due to the genetic homozygosity of the parent lines (see Burton, 1972, for discussion).

Such crossing difficulties are interpreted as meaning that a strong out-breeding system in the American oyster - at least in some individuals in some populations - must be reinforced by a system of gamete cross incompatibility genes. Such systems operate to prevent the crossing of related individuals with similar genes. Incompatibility genes are known to be highly mutable in plants and microorganisms. Interestingly, our gamma-irradiated lines (see more below) are easier to sib-

TABLE 3. Fertilization failures and cleavages in control outcrosses and full-sib crosses of the American oyster[1].

Type of cross	Percent ripe eggs with normal bivalents remaining unfertilized	Percent normal cleavage with 2 polar bodies
Contemporary control outcrosses	0	99
	0	92
	27	62
	25	25
Sib inbreeding crosses	56	5
	77	0
	35	6
	47	0
	39	0
	81	1
	68	1
	93	4
	68	6

[1] From a manuscript to be published in the journal *Cytologia*.

TABLE 4. Total fertilization, effective fertilization, and parthenogenesis in control outcrosses and full-sib crosses of the American oyster[1].

Type of cross	Total percent eggs fertilized	Percent eggs with effective fertilization	Percent eggs in parthenogenesis
Contemporary control outcrosses	90	90	11
	74	74	0
	50	50	0
	88	88	0
	73	61	33
	71	68	13
	22	22	0
	100	100	0
Sib inbreeding crosses	59	31	44
	10	5	34
	60	0	57
	24	5	23
	6	6	0
	14	9	14
	30	24	5
	8	8	3
	11	6	6
	13	8	38
	36	0	31
	35	0	62
	0	0	5
	0	0	91
	3	0	9
	14	14	57
	19	11	38
	18	0	0

[1] From a manuscript to be published in the journal *Cytologia*.

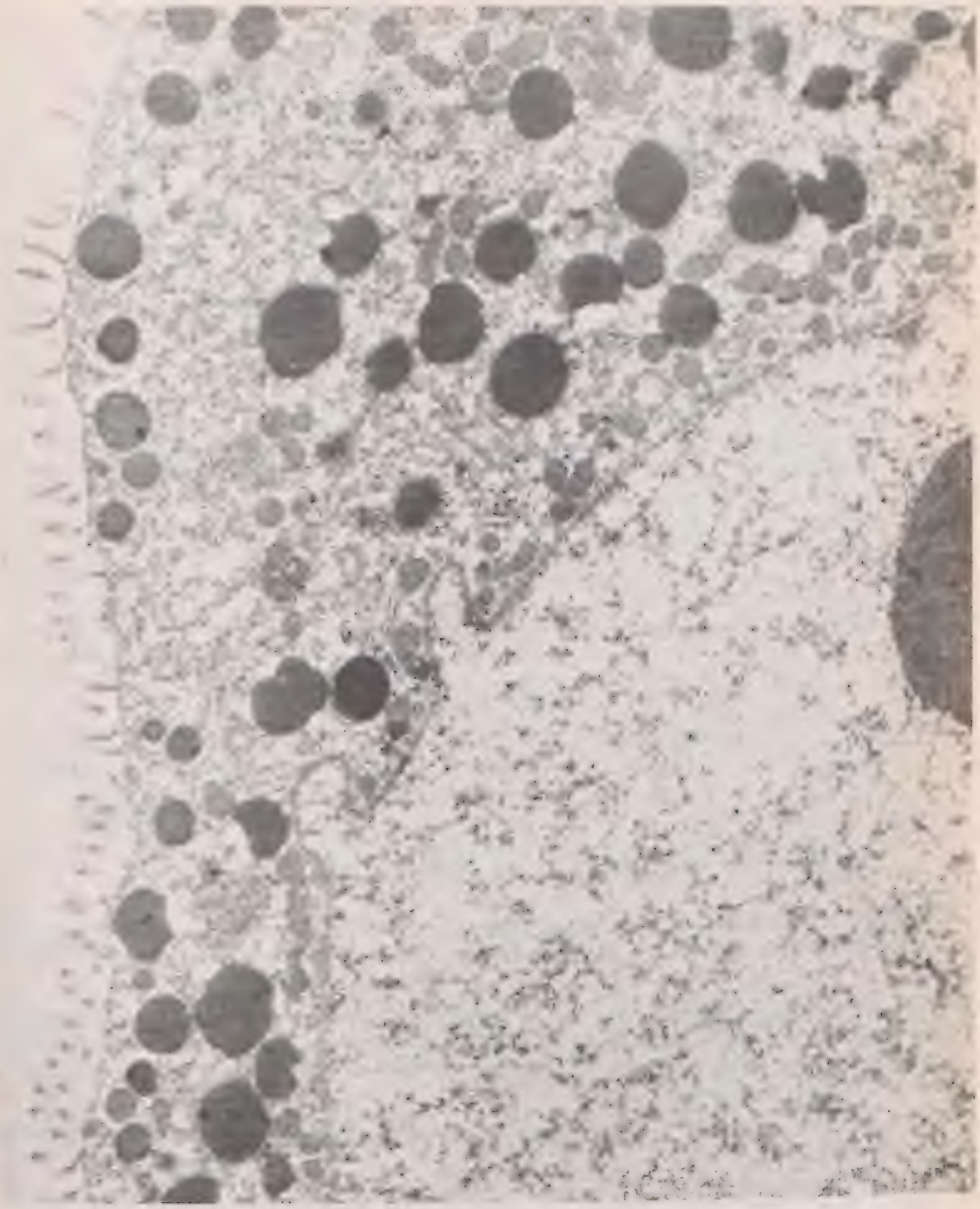


FIG. 8. Section through the American oyster oocyte showing small villi along the surface of the egg, yolk and lipid globules, mitochondria and ribosomes in the cytoplasm, and the nucleus with a portion of a nucleolus showing. X9,095. Courtesy of Dr. E. Daniels, Argonne National Laboratory. (From Daniels *et al.*, 1973).

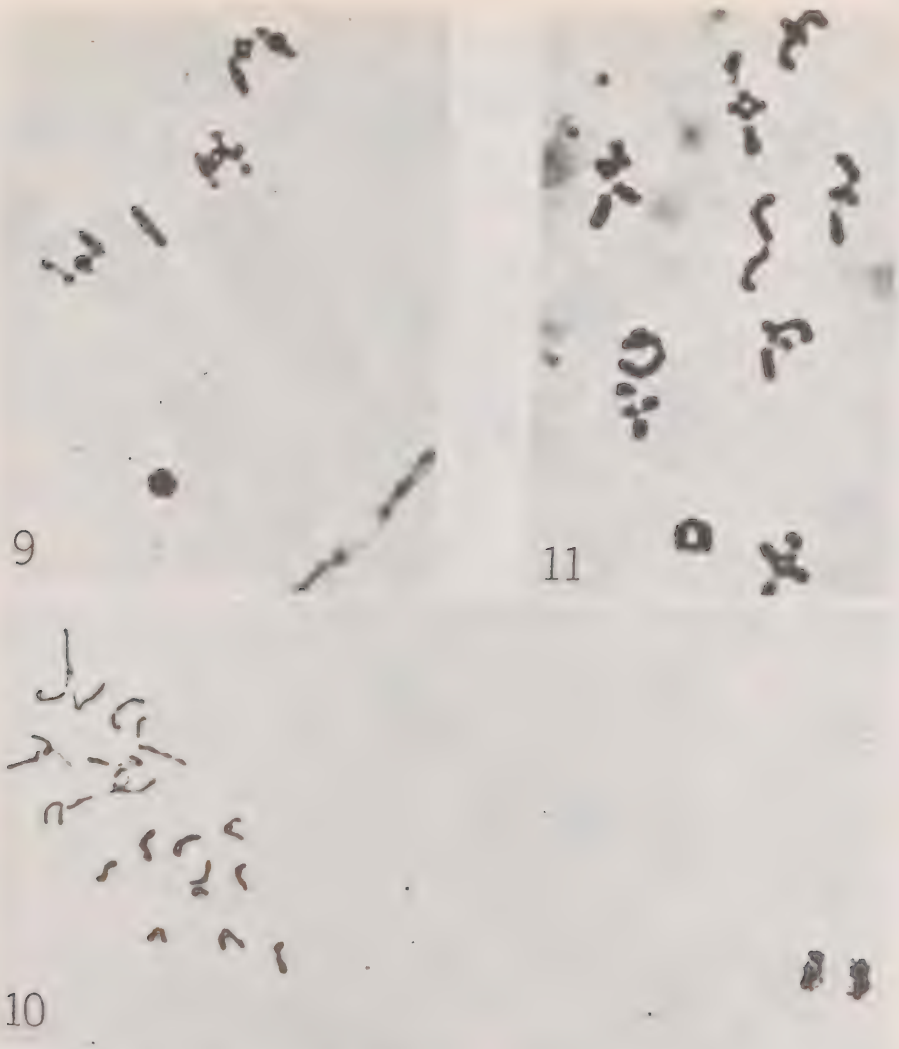


FIG. 9. Fertilized egg of the American oyster showing the 10 pairs of chromosomes lined up on the spindle, with the round, dense, sperm nucleus to one side of the row of chromosomes.

FIG. 10. Two chromosome groups in an American oyster egg - the more contracted chromosomes, from the sperm nucleus, the longer chromosomes contributed by the egg - just before their fusion on the first cleavage spindle. Two polar body nuclei show at one edge of the photomicrograph.

FIG. 11. Prometaphase I of meiosis in an American oyster egg showing the 10 pairs of chromosomes.

cross (unpublished information). It appears that the hermaphroditic bay scallop, *Argopecten irradians*, usually spawns either eggs or sperm thereby avoiding most of the time the risk of self-fertilization. At least in this species of scallop, when both eggs and sperm are shed simultaneously, self-fertilization can occur followed by normal development (Castagna & Duggan, 1971).

Genetic systems of cross incompatibility exist in an estimated 3,000 higher plants (Brewbaker, 1964; Williams, 1964). However, the only carefully analyzed prior case in an animal has been interestingly in a marine organism, the herma-

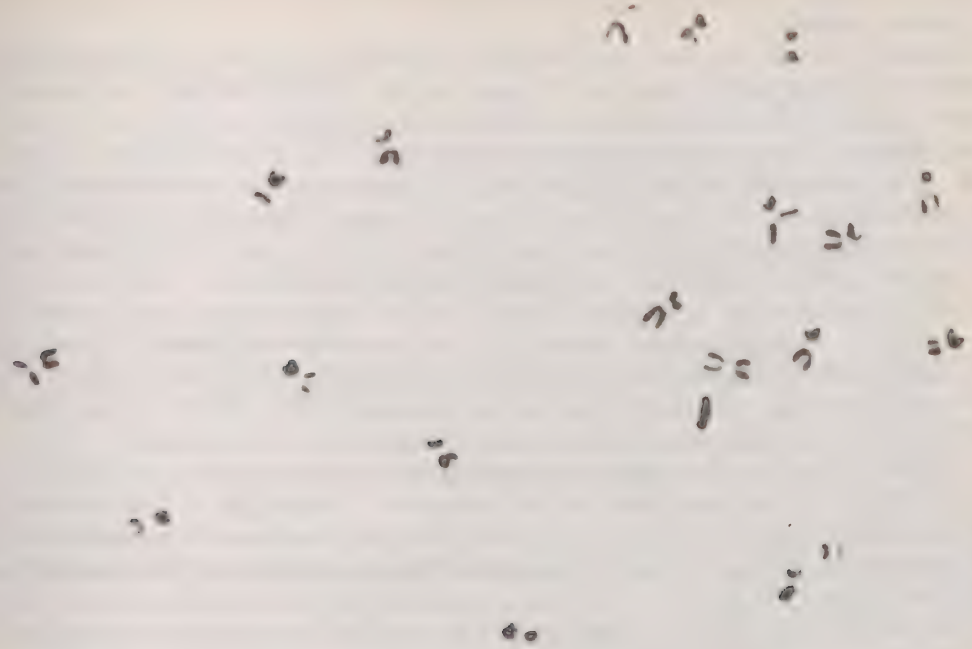
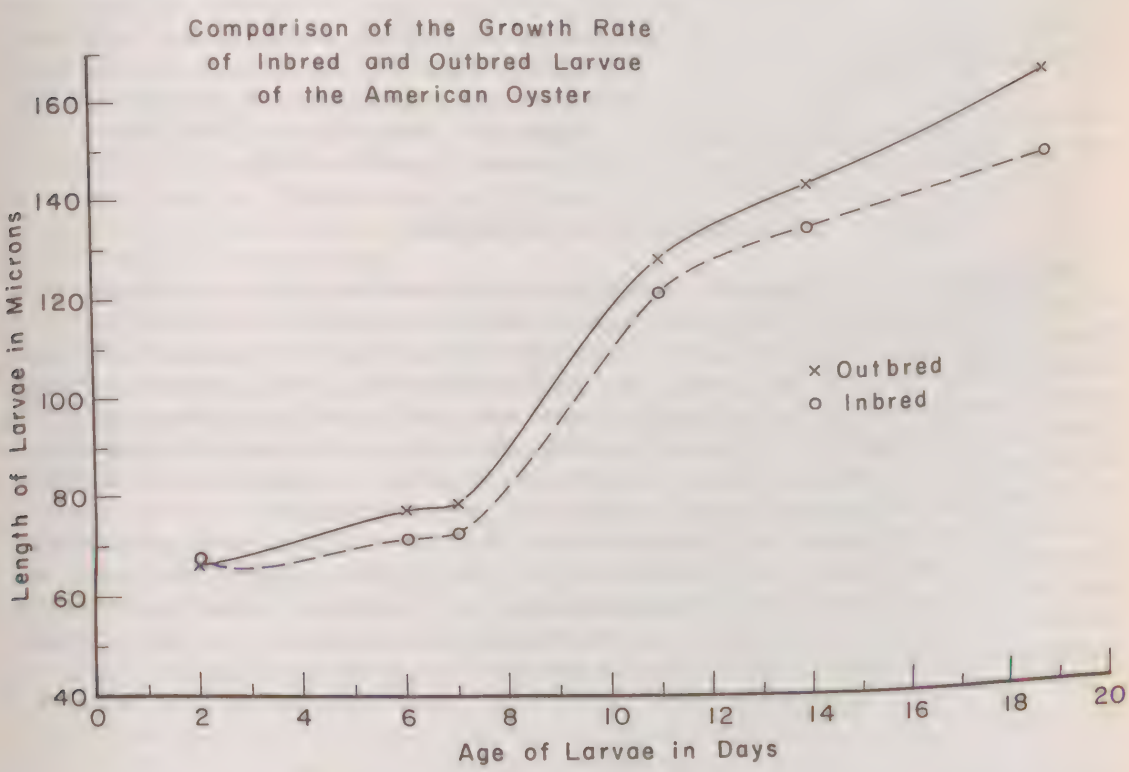


FIG. 12. The 20 chromosomes of a colchicine-treated metaphase of an early cleavage of the American oyster.



phroditic ascidians studied in the early days of genetics by Morgan (1924a, 1924b, 1938, 1942a, 1942b).

Preliminary work on the commercial gastropod abalone revealed that the attraction of conspecific sperm to eggs of this species may be substantially stronger than that for other species (Owen *et al.*, 1971).

Other species having inbreeding incompatibility often have some interspecies gamete incompatibility as well. This might accordingly be expected and has been found to some extent for the oysters (Imai & Sakai, 1961; Menzel, 1967, 1968a). A variety of physical and chemical agents, and other means, can be used to overcome these crossing barriers as done in other organisms. There is a recent report on experimental self-fertilization of the Japanese oyster, *Crassostrea gigas*, using the cryopreserved sperm of sex-reversed oysters (Lannan, 1971). A low incidence of fertilization was obtained. Japanese workers (Imai & Sakai, 1961) were able to sib-cross this oyster for 3 generations before losing the lines. Possibly, *C. gigas* is less resistant to inbreeding than *C. virginica*.

In a highly fecund outbreeding marine species as the oyster a large number of defective genes can be expected to be harbored. Battaglia (1970) found marine copepods to be extremely sensitive to protracted inbreeding. He found inbreeding to have a significantly more severe effect on the marine population tested than on the one from brackish water.

Under carefully controlled conditions, survival of outbred *Crassostrea virginica* was 6 times greater than for contemporary sib-inbred larvae over the period of 12 to 17 days. Differences in larval lengths between inbreds and outbreds became apparent by day 6, with these differences becoming more pronounced as time progressed and having statistical significance (Fig. 13) (Longwell & Stiles, in press)[1].

Imai & Sakai (1961) detected and made measurements of inbreeding depression in the Japanese oyster.

It is generally recognized that inbreeding is becoming a problem now with fish that have been selected some generations for pond culture. It could become a problem in shellfish hatcheries (*FAO Fisheries Report No.* 119, 1972).

SELECTIVE BREEDING

Wild populations of oysters and other marine candidates for aquaculture must be domesticated to make hatchery production competitive with wild set, that is, the wild organism must be made more fit for the artificial aquaculture environment in which it is to be grown. Usually, in outbreeding wild populations there is tremendous genetic variation that will respond to selective breeding. This variation can be used - at the same time the oyster is responding to domestication - to improve the quality of the product and to breed for resistance to diseases which become increasingly harmful under intensive cultivation.

Quantitative, commercially important traits are controlled predominately by exceedingly large numbers of either of 2 types of genes. It is the effect of the one additive type of gene that responds to molding and change by selective breeding. The heritability of a trait is a measure of this additive genetic variance. Heritability estimates can be used to predict progress by selection (Fig. 14).

Good theoretical heritability estimates should be readily obtainable in the oyster

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[1]All statistical work was done by Ruel Wilson of Biometrical Services, Agricultural Research Center, U. S. D. A.

BASIC FORMULA FOR SELECTIVE BREEDING

$$\text{Annual Progress for Trait Being Selectively Bred For} = \frac{\text{Heritability} \times \text{Selection Differential}}{\text{Generation Interval}}$$

$$\text{Heritability} = \frac{\text{Variation Due to Additive Genetic Variance}}{\text{Total Phenotypic Variance}}$$

Selection Differential =
Difference Between Selected Oysters and Average of All Oysters From Which Selected

Generation Interval =
Average Age of Oysters at Time of Reproduction

in 1 generation for any number of commercial traits by crossing the divided lots of eggs of several females by several different males. Contemporaneous cultures of such crosses should provide enough full-sib and maternal and paternal half-sib families for an analysis of variance from which heritability can be estimated directly.

This very desirable method is not practical at the Milford Laboratory because the high incidence of larval mortalities seldom leaves enough families for statistical study. In one series of such crosses of the American oyster enough larval families survived long enough to estimate heritability of larval growth to 2 weeks. This estimate, 24%, is in the medium-to-low range. It is high enough though to expect some improvement by mass selection without immediate recourse to progeny testing or family records.

Much earlier Chanley (1955) attempted to separate environmentally caused variation from genetic variation in the growth rate of larvae of the hard clam, *Venus mercenaria*. Differences were found between larvae from the same female crossed with 2 different males, and also between larvae from 2 separate females crossed with the same male.

Recently, some other heritability estimates largely related to growth parameters were obtained for *Crassostrea gigas* in a commercial-scale pilot hatchery at the University of Oregon. A less precise method which utilizes only full-sib families was used (Lannan, 1972). Different estimates were obtained for shell dimensions of the spat at 12 and at 18 months. Results, like that for growth rate of *C. virginica* larvae, were encouraging in terms of predicted gains by mass selection.

Realized estimates, as contrasted with these theoretical estimates, can be obtained from selection experiments. Such experiments can also tell something about the duration of the response to selection and about the limits of selection for different coefficients of inbreeding and different selection differentials.

Such an experiment was set up with a collection of about 6,000 wild American oysters. Most of these were from Long Island Sound, but some nonlocals were included to increase the base of genetic variability. Of these, 835 spawned, 15% of which were nonlocals.

The first realized heritability figure for growth rate to 33 days postsetting was quite high, 93%, and indicative of considerable gain to be made by hatchery selection for rapid growth of spat under conditions similar to those of this experiment (unpublished work, Milford Laboratory).

Selection progress is being made for resistance to the microsporidian MSX disease of the American oyster in the Mid-Atlantic states by both natural selection on the wild beds and in a small artificially selected experimental stock at Rutgers University by H. Haskin (open discussion at the 1971 Annual Meeting of the National Shellfisheries Association, Seattle, Washington). Over a period of many years the *Crassostrea virginica* oysters of Malpeque Bay, Prince Edward Island, slowly but certainly made themselves resistant to the Malpeque disease through the agency of natural selection (Needler & Logie, 1947).

Hybridization can be a means of obtaining new genetic variability prior to selection.

HYBRIDIZATION

"Wide" introductions of the genes of rare types to those of common types were part of the domestication and cultivation of probably all of our domestic animals and crops. In artificial oyster culture commercial success might await the introduction of genes from the less common to the more common commercial oysters. It is quite probable that unexplored material will offer better qualities which are not now being exploited for aquaculture. More crosses between diverse populations of wild species or even genera should be attempted for the purpose of synthesizing new breeds of oysters for the new methods of intensive artificial culture. For example, hybridization of *Crassostrea virginica* might supply a less sensitive, more vigorous larval form better able to hold up to the vicissitudes of the hatchery.

Hybrids could furnish a diversification of the U. S. East Coast oyster crop. Diversification can break the wildfire spread of a disease by the interdispersal of resistant types. It can assure some marketable crop when the disease toll of the susceptible types is greatest. Disease and parasitic infestations become increasingly harmful with increasing intensification of production, as noted above.

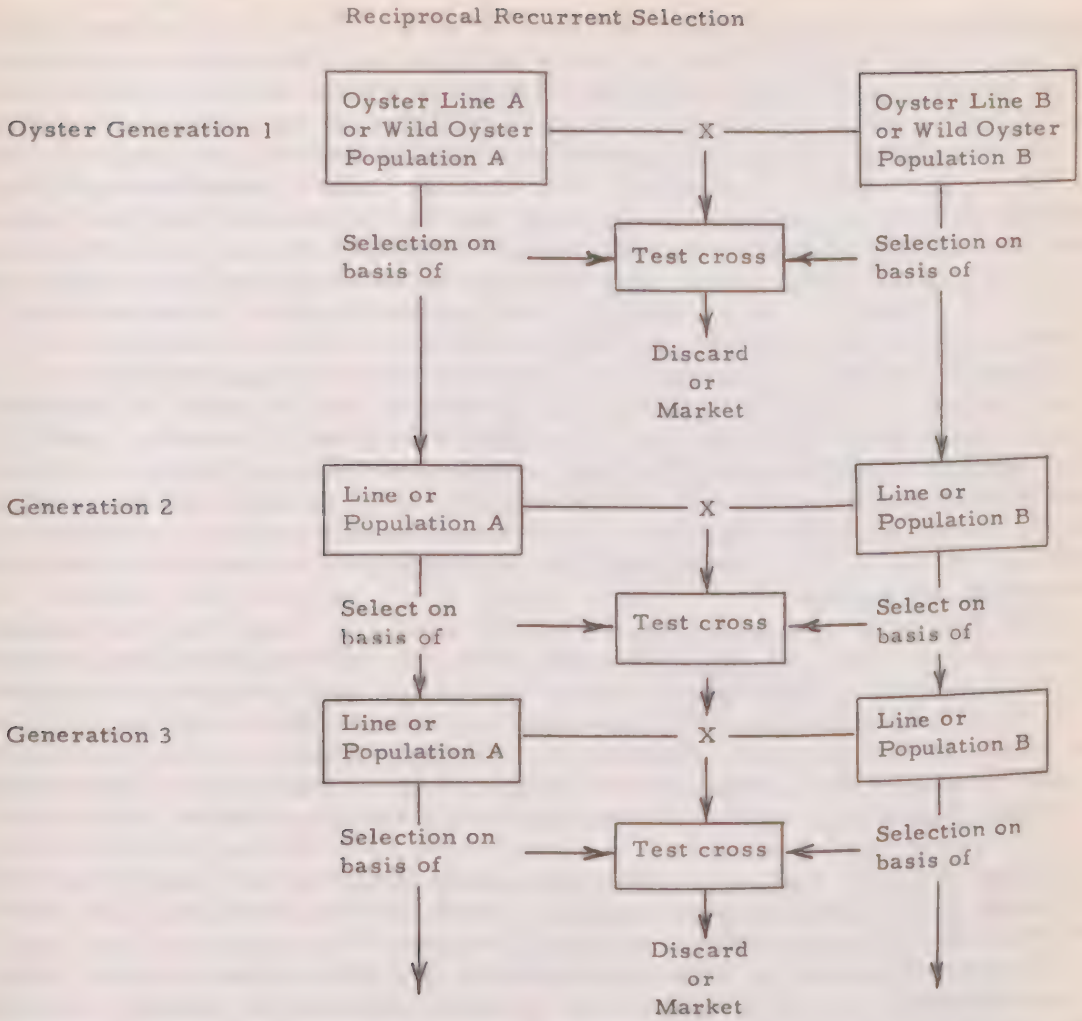
Were more known about the genetics of different geographic populations of the American oyster, some of the fear might be diminished of experimental transplantation of oyster set to commercial beds badly in need of seed from areas where it occurs in great abundance and goes to waste.

Oysters are very dependent on the environment in which they are reared for flavor and quality. New oyster hybrids grown in the environment of the preferred commercial parent should, therefore, generally, be more similar to the native type than would be hybrid higher plants and hybrid higher animals. There should thus be no necessity for creating an entirely new market.

On the basis of occurrence in nature, it seems that hybridization techniques could play in aquaculture a role more akin to the very important one such techniques had in plant breeding than to the lesser one they played in the breeding of higher animals. Factors which limit interspecific crossing in mammals are of little concern in molluscan breeding.

The fecundity of the oyster further should permit, as in plants, the inbreeding, as described above, of large numbers of lines specifically for subsequent hybridization. Hybridization of inbred lines is responsible for the phenomenal successes of maize and chicken breeding. It has not been suitable for the breeding of large individually costly farm animals because of the high mortality rate within the inbreeding lines and the loss of a large number to most of the inbred lines due to the uncovering of lethal recessive genes with the increasing homozygosity that accompanies inbreeding.

Also, once a number of genetically distinct, though not necessarily deliberately inbred hatchery strains are produced, they might likewise be crossbred. This is



a more moderate breeding approach than either inter-species hybridization or the crossing of especially highly inbred strains. Most beef cattle now produced in the United States for market are hybrids of established breeds.

One purpose of crossbreeding or hybridizing is to utilize the effects of hybrid vigor. Unfortunately, there is no way of predicting for any species just where to find hybrid vigor. Mildly inbreeding populations or lines might be test-crossed with one another each generation so that selection can be practiced in terms of the potential of the separate lines for producing heterosis on crossing (Fig. 15).

Hybridization for the sake of combining the desirable genes of 2 different types sometimes takes the form of upgrading practiced when the overall performance of the import is better than the local, but when the local is superior in some particularly important traits related to the local environmental conditions. The initial hybridization is followed by backcrosses to the import with either natural or artificial selection. Another way of combining the characteristics of 2 types is the introgression of desirable foreign genes into the local stocks. This is accomplished by backcrossing the hybrid to the local type with either natural or artificial selection.

Old, well-established subspecies usually have gene combinations so well adapted to the environments they occupy that any new gene combinations created by

hybridization will nearly always be less favorable. The oyster industry's fear of imports has a factual basis in its recognition that oysters transplanted from different geographic areas do not do well in their new environments. Ecological adaptations are common in wild subspecies of just about any organism. Hybridization is an important means of overcoming this. If, moreover, hybridization takes place in an unstable environment, and artificial culture conditions could be so classified, some of the vast array of segregates appearing in later generations will very likely be better adapted to the new conditions than any individual of the parental group. Often, hybrids have increased environmental range, or ability to live in conditions in which either parent is unable to live. There is a tenfold increase in the frequency of naturally occurring species hybrids of the Pacific abalone, a commercial gastropod, in areas subject to habitat disturbances. In some cases natural hybridization was correlated with the rarity of one of the parent species beyond the extreme range limit of the parent (Owen *et al.*, 1971).

Geographic variation among marine animals and the occurrence of polytypic species have been recorded by various authors. Such variation may be the principal, if not exclusive, speciation mechanism in most marine animals (Mayr, 1954). Stenzel (1971) gives examples of geographic, as well as successional speciation in oysters.

The American oyster occurs extensively over an unusually wide range of temperature, from cold to subtropical, along the Atlantic Coast from the Gulf of St. Lawrence to the Gulf of Mexico, and farther south to Panama and around the West Indies (Yonge, 1960). Loosanoff & Nomejko (1951) demonstrated differences in the spawning reaction of different populations in relation to the temperature. Paper partition chromatography showed a reproducible difference in the patterns of free amino acid or small peptides between a population of *Crassostrea virginica* oysters indigenous to Long Island Sound and to the James River, Virginia (Hillman, 1964). In a serological study of species and races of *C. gigas*, Numachi (1962) found the 4 races to have some antigenic differences that are in accord with the degree of their geographic isolation from each other.

Inclusion of nonlocal *Crassostrea virginica* in several of the individual mass-spawned groups already referred to had no measurable adverse effects in respect to percentage fertilization and development of the eggs to the straight-hinge larval stage, mortality, abnormalities and percentage larvae reaching setting (Stiles & Longwell, in press).

Wild *Crassostrea virginica*, sampled from approximately 25 different sites - from areas farmed commercially and nonfarmed areas - from Prince Edward Island to Virginia, are being test-hybridized. Crosses have so far been made of Long Island Sound oysters with oysters from Prince Edward Island; Maine; New Hampshire; Martha's Vineyard, Massachusetts; Niantic and Greenwich, Connecticut; and Fisher's Island, New York. Rhode Island oysters have been crossed with Massachusetts, New Hampshire and PEI wild stock.

To date, culture records show the following:

1) Lack of crossing barriers except possibly between Maine and Long Island Sound.

2) Good performance of all the hybrids as larvae.

3) But outstanding performance of Maine hybrids as larvae and early post-setting spat.

4) For almost all the hybrid crosses - a growth rate of the spat in the first year slower than that of the local controls, but still better than that of the non-local controls.

5) Extremely poor growth of the older spat of Maine hybrids and of the Maine x

Maine controls with total mortality before the second year. Maine hybrids did better though than the Maine control crosses.

6) Although crosses are still small in number, it seems that the Rhode Island x PEI hybrid may be showing marked vigor at the mid-to-late larval stages and at setting after an initial higher than usual mortality of the larvae at the early straight-hinge stage.

Imai & Sakai (1961) found that their races of *Crassostrea gigas* in Japan readily hybridize, and that the F_1 hybrid is fully fertile. Generally speaking, the cross-breds had a higher degree of hardiness, as compared to the inbred strains, and a greater adaptation to environmental conditions.

Cross-fertilization is readily obtained between *Crassostrea virginica* and *C. gigas*, cell division proceeds normally and early veliger larvae are obtained (Galtsoff & Smith, 1932; Davis, 1950; Imai & Sakai, 1961). All larvae were reported, however, to die before reaching the umbo stage. In crosses of *C. gigas* with *C. angulata* a high percentage of fertilization occurred, development was normal and many spat were obtained which showed characteristics of each parent species (Imai & Sakai, 1961). In the cross of *C. echinata* x *C. gigas* the rate of fertilization was low, cleavage was slow and abnormal, and only a few eggs reached an abnormal early veliger larval stage. When *C. gigas* was used as the female instead of male parent a higher percent fertilization was achieved, but larval development, though somewhat better than in the reciprocal cross, was still abnormal and most larvae died in a few hours (Imai & Sakai, 1961). These same 2 workers (1961) reported that almost no cross-fertilization occurred between the common Japanese oyster, *C. gigas*, and *C. rivularis* which occurs in China and Japan. No veliger larvae were obtained. *C. rivularis* has been planted in Puget Sound along with shipments of *C. gigas* seed and has established itself there (Galtsoff, 1964).

More recently, Menzel (1967, 1968a) has made a systematic hybridization study of 6 species of *Crassostrea*. All combinations of crosses resulted in cell cleavage except the crosses with *C. commercialis*. The gametes of this oyster were incompatible with those of all other species. Mitosis in the cleavages of the hybrid zygotes appeared normal except when *C. iredalei* was used as one of the parents. Then sometimes as many as 90% of the cells were anomalous, and haploid, triploid and hexaploid chromosome numbers were present in the cleavages. All the hybrids had some larvae that persisted to the umbo stage, and some went to metamorphosis to produce juvenile oysters which were reared to sexual maturity. It was noted by Menzel that those hybrids in which *Crassostrea gigas* was a parent had greater growth than the others.

Meiosis in the F_1's and cleavage mitoses in the zygotes resulting from crosses of the F_1 with one another and in backcrosses to *Crassostrea virginica* appeared normal in the case of the *C. angulata* x *C. gigas* hybrid and with *C. rhizophorae* x *C. virginica* hybrid (Menzel, 1971a). All the other hybrid types had considerable meiotic abnormalities, and in their F_2 there were mitotic anomalies. *C. virginica* and *C. rhizophorae* are taxonomically quite similar (Galtsoff, 1964).

Cytogenetic examination of an attempted cross of *Crassostrea virginica* with *C. angulata* revealed 35% of the eggs to be unfertilized. Another 10% had a very delayed fertilization. Polyspermy occurred in 35% of the eggs. Sperm nuclei were abnormally large and irregular in 25% of the eggs. Cleavage was irregular in 5%. Nuclei of the early larval tissues were abnormally vacuolated and highly irregular in shape. For detailed data see Stiles (1973).

Results of hybrid trials ought to be interpreted with consideration of the new classification of Stenzel (1971) which places living oysters in more than 3 genera

(Galtsoff, 1964). Stenzel places *Crassostrea commercialis* in a genus apart from the *Crassostrea* and *Ostrea*. This additional genus, *Saccostrea*, differs from *Crassostrea* in its deeper umbonal cavity, strong chomata and in a tendency to form cornucopia-like shapes. *Saccostrea cucullata*, the equivalent of *Saxostrea commercialis* Iredale & Roughley (1933), was also earlier reported by Galtsoff & Smith (1932) as being unable to cross-fertilize *C. virginica*. Further, the eggs of *S. cucullata* have no effect in stimulating spawning of the ripe males of *C. virginica*.

No species hybrids have been attempted in the incubatory genus *Ostrea*. (Larvae are incubated in the gill cavity, see Yonge, 1960.) This is in spite of the fact that this genus contains the commercially important European oyster, *O. edulis*. *O. edulis* has been reared under laboratory aquaculture techniques (Walne, 1966). The eggs of this incubatory species are discharged into the gill cavity (Galtsoff, 1964) rather than spawned into the water. This makes selected artificial hybridization for either experimentation or breeding technically a more difficult, tedious job than with the *Crassostrea* genus.

There have been no genetic studies on any of the deep-sea oysters hitherto regarded by oyster biologists as belonging to the genus *Pycnodonte*. Stenzel (1971) offers evidence for the separate origin of the commercial and non-commercial deep-sea types of oysters at the rank of taxonomic family, as noted briefly above. Study of the deep-sea forms by different methods of genetic analyses, biochemical, chromosomal and trial hybridization, could yield important basic information on the more recent evolution of the common oysters. Such information could have practical applications in breeding programs and in the scientific interpretation of the significance of successes and failures of such.

Northern and southern quahog clams, *Mercenaria mercenaria* and *M. campechiensis*, respectively, hybridize readily in the laboratory and the hybrid is fertile. Growth of the F_1 and F_2 hybrids is similar to that of the faster-growing southern type. Shell characteristics of the F_1 hybrids are intermediate to those of the 2 parents. In the F_2 and F_3 hybrids there is segregation for the shell characteristics. The hybrids have almost as good keeping qualities when removed from the water as the superior northern parent (Menzel, 1971a, 1971b; Chestnut *et al.*, 1957; Haven & Andrews, 1957).

Interspecies hybridization of oysters is taken up as the main theme of another paper of this symposium by R. W. Menzel.

MUTATION AND IRRADIATION

Irradiation can be used to increase the genetic variability and thus speed up genetic gains by selection. Mutation breeding has been scarcely attempted in economically useful farm animals. This is because of the high cost of culling out the large numbers of individuals with the lethal or sublethal mutations that are induced along with the useful ones. Because of the oyster's tremendously high reproductive rate and the insignificant worth of a single oyster, there would be no such limitations on mutation breeding of the oyster. The gross morphological sameness of the oyster and slow conservative rate of evolution, with present day oysters little different from their carboniferous ancestors, make study of induced mutations in this invertebrate of particular interest, as well as of practical value.

Irradiation might be used to sterilize highly selected hatchery strains to hasten somatic growth, induce out of season fattening for market and prevent competitor companies from breeding from the strain all at the same time. It can surely

be used to induce parthenogenesis for inbreeding purposes, perhaps for mass replication of particularly desirable oysters in their female phase. A larval mutant with a larger mouth would be able to utilize a wider range of larger sized algal cells as food and so reduce the food problem in a commercial hatchery.

Studies have been conducted on the breeding response of the commercial American oyster to ionizing radiation (Longwell & Stiles, 1972b; Longwell & Stiles, to be published)[2].

Spawned unfertilized eggs of the American oyster were X-irradiated with 65 to 4,000 R and crossed with untreated sperm (Table 5). Fertilizability of the eggs was not reduced, but cleavages were delayed somewhat. Starting with 500 R cytogenetic abnormalities were frequent, indicating a moderate sensitivity compared to some lower animals, but a low one relative to higher animals. It takes 100,000 R to inactivate trout, plaice and flounder eggs (*Fish. Lab. Ann. Rept.*, Lowestoft, Suffolk, England, 1969), while 8 R is lethal to a human oocyte (*Rept. U. N. Scientific Committee A*/6314).

Pooled sperm of several oysters was X-irradiated from 125 to 10,000 R and crossed with untreated eggs (Table 6). It takes 10,000 R to induce all abnormal larvae. This occurs in the more sensitive common killifish at 2,000 R (Solberg, 1938). The oyster sperm is sensitive to the induction of dominant lethal mutations, this occurring in the same range as for the far more generally sensitive mammals, about 300-750 R (*Rept. U. N. Scientific Committee A*/6314). Total larval mortality occurs when the sperm receives 5,000 R. By contrast, sea urchin sperm can sustain 120,000 R (Speidel & Cheney, 1962). Irradiating the oyster sperm reduces larval growth at the same dose range as it does for irradiation of snail eggs, about 1,000 R (Bonham, 1949). No juvenile oysters were obtained at 3,000 R.

In terms of the reduction of the mid-life of the adults, gastropod mollusks display a great insensitivity to ionizing radiation of the same order of magnitude as the arthropods (Polikarpov, 1966). The pelecypod mollusks are probably still more resistant (Price, 1962). The LD_{50} for mollusks is roughly 10 times that for mammals.

Cesium 137 gamma rays in the wide range employed to adult oysters - 65 to 10,000 R - did not induce sterility (Fig. 16). Rather, it hastened sexual maturity and probably the total production of gametes. The gastropod *Physa* has a temporary sterility with 10,000 R. Permanent sterility is induced at 100,000 but 9,000 R will permanently annul fecundity in the very young (Ravera, 1966). Dosimetry studies done at the Brookhaven National Laboratory show that the American oyster shell reduces the amount of irradiation reaching the oyster meat by a maximum of 12%[3].

About 20 crosses were made from the spawn of these gamma-irradiated adults. Results are summarized in Table 7.

At high doses there was a reduced percent development of the spawned eggs to the first larval stage. Abnormalities of larval form and behavior, and atypical shading of the larvae occurred at moderate and high, but not lower doses with the exception of one parameter. At moderate and high doses, there was a marked increase in larval mortality. Growth rate of the larvae was improved at low

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[2]All of the irradiation was done at the Brookhaven National Laboratory, Brookhaven, Long Island, New York, through the assistance of Dr. Arnold Sparrow.

[3]Dosimetry studies were conducted in the laboratory of Dr. Arnold Sparrow, Brookhaven National Laboratory, Brookhaven, Long Island, New York.

TABLE 5. Numbers of cleavage abnormalities in embryos from an American oyster cross of X-irradiated eggs x untreated non-irradiated sperm.

Dose 68.8 R per min	Ten embryos examined for each control and each dose									
	Total no. mitoses	Unfertilized eggs	Delayed cleavages	Hetero-ploidy	Pale and/or pyknotic nuclei	Ball-type meatphases	Micro-nuclei	Single & multiple bridges	No. of embryos with 1 or more abnormalities
0	87	3	-	-	-	-	-	-	0
0	94	2	-	-	-	-	-	1	1
0	91	-	-	-	-	-	-	1	1
65	37	4	-	-	-	-	-	-	0
125	52	-	-	1	-	-	-	-	1
250	74	-	-	-	-	-	-	1	1
500	84	1	-	-	-	-	-	3	3
1000	35	-	1	-	-	-	-	2	3
2000	50	-	-	1	-	-	1	9	9
3000	56	-	-	-	2	-	2	7	10
4000	49	-	-	1	5	1	2	8	10

doses. Of the larvae that survived, there was an improved rate of metamorphosis to the adult form at all dose ranges. Some of the peculiar characteristics of the cultures of Irradiated x Irradiated were absent in the Irradiated x Control crosses. For other parameters the effect persisted.

In respect to the larval growth rate and percent of metamorphosis of surviving larvae to the adult form, there was a very marked heterotic effect when an

TABLE 6. Culture history of crosses of X-irradiated pooled sperm of the American oyster x non-irradiated eggs.

Dose 1194 R/min[1]	Percent development of eggs to 1st larval stage	Percent 1st-stage larvae abnormal	Percent mortality 1-week larval culture	Age in days at beginning of metamorphosis	Numbers of juvenile oysters surviving 1 year
0	27	25	<5%	26 days	1167
0	16	53	<5	26	Accidental loss
0	30	23	<5	26	1151
125	25	12	<5	26	1057
250	20	27	5	26	Accidental loss
500	16	46	10	26	1022
1000	25	24	10	28	790
2000	16	45	10-15	33	468
3000	15	53	15	35	7
4000	15	69	10	40	0
5000	2	95	25	-	0
7500	0.5	80	100	-	0
10,000	0.2	100	100	-	0

[1] Data for each class based on fertilization of 140,000 eggs.

irradiated oyster was crossed with a non-irradiated oyster.

Cytological study of some of the F_2 within-culture crosses of the original gamma-irradiated oysters shows cytological abnormalities to be 1.7 times as frequent as in the control group crosses. The largest category of abnormality was heteroploidy, which ranged all the way from hypo-haploidy to hyper-tetraploidy.

TABLE 7. Culture profile of crosses of American oysters after whole-body irradiation.

Culture characteristic	Dose range in which characteristic appears in Irr x Irr crosses			Irr x Control crosses
	65-750 R	1000-2500 R	3000-10,000 R	
Reduced development of eggs			x	Normal for all doses
Unusual abnormalities of larvae		x	x	Absence of class with gross malformations
Shell irregularities		x		Same as Irr x Irr
Aytpical longevity of abnormals		x	x	Same as Irr x Irr
Atypical larval colors		x	x	Not clear if different from Irr x Irr
Superactive larvae	x	x	x	No superactive culture for any dose
Abnormal swimming patterns		x		Same as Irr x Irr
Increased, high or total larval mortality		x	x	Mortality insignificant
Abnormal large range of larval sizes		x	x	Same as Irr x Irr
Improved larval growth rate	x			Improved to excellent in crosses of high doses x C
Improved metamorphosis rate	x	x	x	Improved to excellent
Improved juvenile growth	No measured difference over controls			Excellent

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FIG. 16. Adult American oyster set up for gamma-irradiation at the Brookhaven National (AEC) Laboratory. Photograph courtesy of Dr. Arnold Sparrow of the Brookhaven Laboratory.

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HYBRIDIZATION IN OYSTERS (*CRASSOSTREA*)

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ABSTRACT

Twelve species of *Crassostrea* from various areas of the world were available for study, including the local *C. virginica* and all the other principal commercial species. Seventy-two reciprocal crossing attempts were made of the possible 132 combinations. All crossing attempts were duplicated (as many as 12 times in some combinations), making a total of 282 attempts, and attempts were made to rear 98 of these. Seven of the species were completely infertile with all other species or showed less than 5% fertilization. Cross fertilization (cell cleavage and embryo development) occurred in crosses involving 5 species. Rearing hybrid embryos through to metamorphosis and attachment was successful with 4 species (*C. angulata*, *C. gigas*, *C. rhizophorae*, *C. virginica*). Although the 5th species (*C. iredalei*) had reciprocal fertilization with the other 4, cytological examination showed chromosome anomalies and the embryos never lived beyond 5 days.

The above observations showed that 5 species of *Crassostrea* have close genetic affinities, but *C. iredalei* is more distantly related to the other 4 than they are to each other. Judging from ease of crossing, rearing larvae through metamorphosis, chromosomal behavior and morphological similarity, the closest relationships are between (1) *C. angulata* and *C. gigas* and (2) *C. virginica* and *C. rhizophorae*. It is concluded tentatively that *C. angulata* is a subspecies of *C. gigas* and that *C. rhizophorae* is a subspecies of *C. virginica*.

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ONCOMELANIA HUPENSIS (GASTROPODA: HYDROBIIDAE) HYBRIDIZATION, GENETICS AND TRANSMISSION OF *SCHISTOSOMA JAPONICUM*[1]

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ABSTRACT

A model is presented for studying the infraspecific molluscan genetic mechanism(s) governing the transmission of the Oriental human blood fluke, *Schistosoma japonicum*. The Japanese strain of parasite was used. Male, parasite-resistant, smooth, small, albino *Oncomelania hupensis formosana* from southern Taiwan were mated with female, susceptible, ribbed, large, pigmented *O. h. hupensis* from mainland China.

F_1 and F_2 generations were produced. Production of F_1 cross snails was significantly lower than that of the control inbred subspecies; however, this was due to females not being fertilized, not to lowered output of young per female per month. Fecundity of $F_1 \times F_1$ crosses was equal to or greater than that of the control inbred subspecies.

The F_1 generation was equal in size to parental *Oncomelania hupensis hupensis*, was pigmented and had gradation in strength of ribbing suggesting multiple allelic control of the last trait. The F_2 generation exhibited a 9:3:3:1 ratio of pigmented-ribbed:pigmented-smooth:albino-ribbed:albino-smooth. The F_1 generation and all classes of F_2 generation were susceptible to infection at the same level as parental *O. h. hupensis*, i.e., 1.6 ± 0.4%. Genes governing susceptibility are on a chromosome other than that controlling albinism or ribbing.

INTRODUCTION

The interaction of the Oriental gastropod species *Oncomelania hupensis* and the human blood fluke *Schistosoma japonicum* is of considerable interest to those concerned with mechanisms governing snail transmission of the disease and to students of evolutionary biology.

It has long been established that the survival of the geographic "strains" of *Schistosoma japonicum* is dependent on their penetrating and developing in snails of very specific genotype(s) within the species *Oncomelania hupensis* (DeWitt, 1954; review of Chiu, 1967). For example, the Japanese "strain" of the parasite will develop in *O. h. nosophora* from Japan, *O. h. hupensis* from mainland China,

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O. h. chiui from Taiwan, but not in *O. h. formosana* from southern Taiwan or *O. h. quadrasi* from the Philippines. It will infect very few individual *O. h. formosana* from central or northern Taiwan.

The subspecies of *Oncomelania hupensis* were considered distinct species until 1967 when their systematic status was clarified (review of Davis, 1971). A major factor in considering the taxa as subspecies is their potential to interbreed and produce fertile hybrids. Moose & Williams (1963) and Chi *et al.* (1971) initiated hybridization studies to determine whether or not one could discern if the ability to transmit *Schistosoma japonicum* was an inherited trait. Results of Chi *et al.* (1971) indicate that susceptibility is inherited; transmissibility is a dominate factor and refractiveness is recessive in *O. hupensis*.

Richards (1970) pointed out that "little is known about molluscan genetics; studies are urgently needed in particular on the role of genetics in the transmission of diseases by Mollusca and in molluscan systematics." In his 1970 review he discussed what was known about the genetics of *Biomphalaria glabrata* and the role of this species in transmitting *Schistosoma mansoni*. He covered numbers of markers he had discovered in *B. glabrata* of use in cross-breeding studies.

Aside from the initial studies of Wagner & Chi (1959) and Chi *et al.* (1971), work with *Oncomelania* has not reached the level attained with *Biomphalaria*. There has been a need for an ideal model for studying the genetics of *Oncomelania* and the genetics of schistosome transmission. One purpose of this paper is to present such a model where small, smooth, albino, resistant *O. hupensis formosana* were mated with large, ribbed, pigmented, susceptible *O. h. hupensis*. The challenging parasite was the Japanese "strain" of *Schistosoma japonicum*. Emphasis is on results with both F_1 and F_2 hybrid generations.

A further goal is to determine the degree of fecundity and survival of the snails in cross cultures. The degree of success in fecundity and survival of F_1 snails is important in considering the so-called "historical" species of *Oncomelania* to be subspecies of *Oncomelania hupensis*. Quantitative data have not previously been reported on the fecundity of the F_1 generation nor has the extent of mortality of F_1 snails been documented.

MATERIALS AND METHODS

Source of Snails

Albino *Oncomelania hupensis formosana* originated from the Kaohsiung area of southern Taiwan. They were maintained in the laboratory for about 10 generations before use in the experiments reported here which were initiated in September, 1968. *O. h. hupensis* were of the Vogel inbreed strain which came to the 406th Medical Laboratory, Japan, from the laboratory of Dr. H. van der Schalie, University of Michigan, U.S.A. They had been maintained for 3 generations in Japan.

Other taxa used in the infectivity experiments were: *Oncomelania hupensis formosana* from I-lan, northeastern Taiwan; *O. h. formosana* from Pu Yen, contral Taiwan; *O. h. nosophora* from the Kofu Valley, Yamanashi Prefecture, Japan. These snails were third or fourth generation snails.

Snails used in breeding cultures were 2 to 3 months old.

Cultures

Breeding, rearing and holding cultures were in 9 cm Petri dishes of Davis & Iwamoto (1969) as fully reviewed by Davis (1971). Ten breeding cultures were established for each control parental taxon (e.g., *formosana* x *formosana*) and crosses (e.g., *formosana* x *hupensis*, F_1 x F_1). Crosses involved 2 female *Oncomelania hupensis hupensis* x 3 male *O. h. formosana;* 2 female F_1 x 3 male F_1. Control cultures had 3 females and 3 males.

Each month, all young (dead and alive) were removed from the cultures. Those at the 2.5 whorl stage were placed, 1 per culture, into rearing cultures. At the end of 2 months the sex of each individual was determined (method of Wong & Wagner, 1954). Females were placed in different holding cultures than males, 5 per culture. Before cross cultures were established, the sex of all individuals of a holding culture was again determined. Snails used in cross cultures were at least 3 months old and had fully formed varices. F_1 and F_2 snails were scored for phenotype. Each phenotype was maintained separately.

Measurements

Measurements of shell length, length of body whorl, and width were made using a dissecting microscope fitted with a standard ocular micrometer. The number of whorls was recorded and notes taken on the extent of apical whorl erosion. It was noted that after 3 months, 1.0 to 2.5 nuclear whorls were nearly always eroded away, thereby offsetting the potential of making definitive use of the measurement of shell length. Table 5 was constructed by adding 1.5 whorls to eroded shells to enable estimates of whorl number for "entire" shells. The error of ± 0.5 whorls is probable. Similarly, the reader may add 1.5 whorls to data for eroded shells in Table 4 to obtain the probable maximum whorl number.

The degree of ribbing was recorded from F_1 and F_2 shells.

Infectivity Experiments

Three separate experiments were performed testing the susceptibility of various taxa. Snails were placed singly in glass cups (4 ml capacity) containing aged, dechlorinated, previously aerated tap water. Five newly hatched miricidia were pipetted into each cup. Snails were maintained totally submerged for 10 to 12 hours after which they were removed and placed in holding cultures, 5 per culture. *Oncomelania hupensis hupensis*, *O. h. nosophora*, albino *O. h. formosana*, Pu Yen *O. h. formosana*, and F_1 snails were tested in all experiments.

Snails were examined under light for shedding following a period of 10 to 12 hours of drying at room temperature. Such examinations took place at weeks 12, 14, 15, 16 and 18 after exposure to miricidia. At the 18th week, all non-shedding snails were crushed and examined for infections. Control snails were placed in holding cultures to determine mortality of non-infected snails. Holding cultures were examined daily and snails which had just died were dissected to determine if they were infected.

Statistics

Statistical comparisons involved the Students "t" test and coefficient of correlation "r". Significance was accepted at the .05 level.

RESULTS

Fecundity and Mortality

The following conclusions are evident from Tables 1 and 2: 1) The production of F_1 snails was significantly lower compared to production in control or F_1 x F_1 cross cultures when all months were considered. 2) This low production was due to 70% of the *formosana* x *hupensis* cross cultures being barren. 3) Those females that did reproduce did so at rates not significantly different from control parental females. This fact is derived from column 2 of Table 1 where 5.86 young/female/month (y/f/m) was recorded from only those months and cultures where young were produced. 4) Production of young by F_1 x F_1 crosses was equal to that by control female *formosana* and to *formosana* x *hupensis* crosses, but it was significantly greater than that of control female *hupensis*.

Note that the mortality of young (column 5, Table 1) was greater in control cultures than in cross cultures (more than double). Coupling mortality and fecundity data of Table 1, and considering the 1000 females in control and cross cultures, this theoretical condition is proposed:

1) *Oncomelania hupensis hupensis* would produce 1920 young in one month which would survive to maturity.

2) *Oncomelania hupensis hupensis* females crossed with *O. h. formosana* males would produce 544 young in one month which would survive to maturity.

3) The reproductive capacity of the cross female to produce an F_1 generation is 28% that of control females. Considering the mortality and fecundity of F_1 females, 2826 young would be produced which would survive to maturity; this is 1/3 greater than that of control *hupensis*.

Data compiled in Table 3 were primarily derived from the literature and document the variability of fecundity of *formosana* and *hupensis* in different laboratories with different rearing methods. Production is calculated for only those months and cultures where young were produced. The fecundities of the 2 taxa as given in the table are not significantly different. The data serve to indicate the magni-

TABLE 1. Reproduction and mortality rates of *Oncomelania hupensis hupensis*, *O. h. formosana* and their hybrids.

Taxon	Production of young per female per month			Young dead in culture (%)	Female deaths (%)	% Cultures not producing young
	Average for productive months only	For months 1-6 (all 10 cultures)	Greatest for 1 culture in 1 month			
O. h. formosana (control)	4.27 (3.65±0.78)*	3.20 ± 0.74	18.33	40.6	10.0	0
O. h. formosana (control)	6.63 (5.79±1.15)	5.75 ± 1.33	24.00	49.1	30.0	0
hupensis X *formosana*	5.86 (5.86±2.71)**	0.68 ± 0.47	19.00	20.6	0	70
F_1 X F_1	8.77 (9.72±1.85)	6.28 ± 1.45	47.00	55.2	20.0	0

*for statistical analysis the figure in parenthesis is the average for the first 25 months where young were produced starting with counting all months with data in culture 1, followed by culture 2, etc.; i.e., N=25
±the standard error of the mean
**N=7

TABLE 2. Statistical* comparison of reproductive rates of *Oncomelania hupensis hupensis*, *O. h. formosana* and their hybrids.

	O.h.h.	*O.h.f.*	*h.* × *f.*	F_1 × F_1
O. h. hupensis		NS	NS	SD
O. h. formosana	NS		NS	NS
h. × *f.*	SD	SD		NS
F_1 × F_1	NS	NS	SD	

young per female per productive months only

young per female per month (all months)

*N=25, mean and standard error from Table 1.

TABLE 3. Reproductive rates of *Oncomelania hupensis hupensis* and *O. h. formosana* documented in the literature.

Taxon	Length of observation (months)	y/f/m per producing female for productive months*	Author
O. h. formosana	4.5	21.3	Chi & Wagner, 1957
	12.0	11.1	van der Schalie & Davis, 1968
	4.0	4.4	Chi et al., 1971
	9.0	13.6	Chi et al., 1971
	6.0	6.6	this paper
		$\bar{X}$ = 11.4	
		Sd = 6.61	
		Se = 2.97	
O. h. hupensis	12.0	3.2	van der Schalie & Davis, 1968
	6.0	4.3	this paper
		$\bar{X}$=3.73	
		Sd= .77	
		Se= .55	

*where data were gathered for 4 or more months.

$\bar{X}$= mean
Sd= standard deviation
Se= standard error of the mean

TABLE 4. Shell dimensions of *Oncomelania hupensis hupensis* (w), *O. h. formosana* (a), and their F_1 hybrids.

Taxon	Sex	No.	Mean Length	Mean Width	Mean Length of Body Whorl	No. Whorls
O. h. hupensis	♀	10	7.46 ± 0.19	3.15 ± 0.09	3.97 ± 0.09	6.0 - 6.5 e
	♂	10	6.94 ± 0.14	2.97 ± 0.06	3.79 ± 0.06	6.0 - 6.5 e
O. h. formosana	♀	15	6.14 ± 0.08	2.91 ± 0.04	3.81 ± 0.04	5.0 - 5.5 e
	♂	16	5.73 ± 0.08	2.90 ± 0.03	3.71 ± 0.03	5.0 - 5.5 e
Uneroded F_1	♀	3	7.90 ± 0.59	3.41 ± 0.10	4.03 ± 0.18	8.0 - 8.5
	♂	13	7.32 ± 0.08	3.19 ± 0.08	3.90 ± 0.29	7.5 - 8.5
Eroded F_1	♀	10	7.34 ± 0.16	3.32 ± 0.05	3.95 ± 0.04	6.0 - 7.0 e
	♂	10	6.85 ± 0.17	3.14 ± 0.07	3.84 ± 0.05	5.0 - 6.0 e

a= albino
w= wild
±= standard error of the mean

e= eroded apex; loss of 1 1/2 - 2 whorls

TABLE 5. Percentage of fully mature F_1, F_2 generation snails at each whorl stage calculated on the basis of adding 1.5 to the whorl count of shells (77%) with apical erosion.

	WHORLS						
F_2 females of:	5.5	6.0	6.5	7.0	7.5	8.0	8.5
Albino-smooth	0	8	17	0	50	17	8
Albino-ribbed	0	0	18	9	36	23	14
Pigmented-ribbed	0	4	0	16	40	12	28
Pigmented-smooth	0	4	32	40	16	16	8
F_2 males of:							
Albino-smooth	8	0	39	15	23	15	0
Albino-ribbed	9	14	14	9	27	22	5
Pigmented-ribbed	8	0	0	24	28	28	12
Pigmented-smooth	0	0	16	16	48	20	0
F_1 males (all uneroded)	0	0	7	13	27	33	20
(eroded)		4	32	4	40	0	12
F_1 females (all uneroded)						33	67
(eroded)	0	0	44	4	40	0	12

tude of results one could expect in culturing these snails anywhere using a range of techniques.

Shell Dimensions

Shell measurements of male and female *Oncomelania hupensis hupensis*, *O. h. nosophora* and their F_1 are given in Table 4. Adequate measurements of shell length cannot be made because of the erosion of the apical 1.0 to 2.5 whorls. Measurements of the largest size class as determined by the greatest number of whorls are given. The degree of erosion was equal for all taxa (see materials and methods section). On this basis, the shells of *O. h. hupensis* were significantly longer and with more whorls than albino *O. h. formosana*. The F_1 generation had shells significantly longer than albino *O. h. formosana*, but they were equal to parental *O. h. hupensis* (also in number of whorls).

Size differences were not uniformly reflected by length of body whorl or shell width: 1) Female *Oncomelania hupensis formosana* and *O. h. hupensis* were sig-

nificantly different in shell width while males were not. 2) The above taxa did not differ in length of body whorl. 3) F_1 males and females had significantly greater widths and lengths of body whorl than male and female *O. h. formosana*, but did not differ significantly from either sex of *O. h. hupensis*.

The dimensions of F_2 shells ranged from *Oncomelania hupensis formosana* through *O. h. hupensis*. The percentages of male and female F_1 and F_2 shells attaining each of several whorl stages from 5.5 to 8.5 are given in Table 5.

Phenotypes of F_1 and F_2 Snails (Fig. 1)

F_1 snails were uniformly pigmented. There was variation in ribbing with 9% lacking ribs, 26% with very faint ribs, 15 % having low but clearly discernable ribs and 6% with strong ribs (No. = 56).

As shown in Table 6, there were 4 phenotypes in the F_2 generation. The percentages reflected a typical Mendelian di-hybrid cross. Pigmentation and ribbing were dominant factors. The quality of ribbing varied from strong to weak.

Infectivity

Results from the 3 experiments are recorded in Tables 7 to 9. A summarization of data pertaining to taxa studied in all 3 experiments is given in Table 10, along with data of pertinent, previously reported data. The following facts are derived from these tables:

1) *Oncomelania hupensis nosophora*, serving as control for infectivity of the Japanese strain, supported a 79.3% level of infection.

2) *Oncomelania hupensis hupensis* was 2.0% susceptible.

3) Albino *Oncomelania hupensis formosana* was refractive as were I-lan snails of this species.

4) Very few central Taiwan (Pu Yen) *Oncomelania hupensis formosana* could be infected.

5) F_1 snails were susceptible at the same level as *Oncomelania hupensis hupensis* (3.3%).

6) Overall, mortality of experimental snails did not differ greatly from mortality of control snails.

All phenotypic classes of F_2 generation snails were susceptible (Table 9). Two of these, albino-smooth and pigmented-smooth, were infected at percentages 3 to 5 times greater than in *Oncomelania hupensis hupensis*. However, there is an inverse relationship between the number of snails used in the experiment and the percentages of infections. The coefficient of correlation ("r") was -.95 (P = .05). The inverse correlation is significant. Too few snails were available for adequate documentation of susceptibility trends in the F_2 phenotypes.

DISCUSSION

Fecundity and Mortality

Genetic manipulation of populations of *Oncomelania* in order to control the transmission of *Schistosoma japonicum* is worthy of consideration. Once the intramol-

FIG. 1. *Oncomelania hupensis hupensis* (top left 4), *O. h. formosana* (top right 4) and their hybrids. The middle row is of F_1 shells, the lower of F_2 shells. The shell at top left is 7.5 mm long; remaining shells are proportional. Shells on the bottom row were from the 4 phenotypic classes. These are, left to right, pigmented ribbed, pigmented smooth, albino ribbed, albino smooth.

FIG. 1

TABLE 6. The frequency of phenotypes of 167 F_2 snails compared with expected frequencies.

Trait	Actual Frequency	Expected Frequency
Pigmented, ribbed	89.0	94.0
Pigmented, smooth	33.0	31.3
Albino, ribbed	36.0	31.3
Albino, smooth	9.0	10.4

luscan genetic mechanism governing the transmission is known and isolated it may be possible to develop inbred strains of snails of a desired genetic composition. Of importance is the fact that *Oncomelania* is a prosobranch snail where sexes are separate (contrasting with *Biomphalaria glabrata*, a hermaphrodite transmitting *Schistosoma mansoni*). Also, once fertilized, taxa of *Oncomelania* can continually fertilize eggs throughout their lives, which, in the field, average about 2.5 years. Thus it may be possible to commit a female to a lifetime of producing offspring having a predetermined genotype as contributed by a single male.

Data from these experiments indicate that the intrinsic rate of natural increase of F_1 and F_2 snails is sufficient to assure survival and rapid increase in the hybrids. Fecundity in the initial cross females was decreased by 72%, but this was due to non-fertilization in the first 5 months. As time progressed, experience showed that more females produced young. The actual reproductive potential of fertilized females was not decreased when crossed with, and fertilized by, males of the other subspecies.

By comparison with the data presented here, Wagner & Chi (1959) found that *formosana* x *formosana* (control) cultures produced 4.40 y/f/m over a 4 month period while *formosana* x *hupensis* produced 1.88 y/f/m over a 24 month period. The data were for producing females only. Considering producing and barren females, the respective data were 3.95 y/f/m and 1.52 y/f/m. Data were not available for *hupensis* x *hupensis*.

Wagner & Chi (1959) had 80% successful crosses between female *hupensis* and male *formosana*, contrasting with the 30% reported here. Wagner & Chi's results showed that greater success can be attained; it should, however, be noted that great fluctuation in productivity between cultures of the same subspecies is a fact of life in dealing with *Oncomelania* (van der Schalie & Davis, 1968, p 350). Also, while more females produced young in Wagner & Chi's experiments, more young per producing female resulted in this study (1.88 y/f/m contrasted with 5.86). And, as noted in Table 3, the standard error of the mean y/f/m considering different laboratories may be as great as 2.97 and the difference between our data may not be significant.

TABLE 7. Results of experimentally infecting 6 different groups of snails with the Japanese strain of *Schistosoma japonicum*. Emphasis is on results with F_1 snails.

Snails	Experimental				Control	
	No.	Surviving (%)	Infected A (%)	Infected B (%)	No.	Surviving (%)
Oncomelania hupensis hupensis	60	96.7	3.33*	3.45	20	90.0
O. h. formosana, a	60	75.0	0	0	20	75.0
O. h. formosana, I-lan	60	78.3	0	0	20	90.0
O. h. formosana, Pu-Yen	60	98.3	1.66**	1.79	20	95.0
F_1	80	88.7	1.25**	1.41	20	80.0
O. h. nosophora	80	47.5	41.3***	86.8	20	60.0

a, albino
A, infection in terms of number of snails at the beginning
B, infection in terms of surviving snails
*, 1 by shedding, 1 by crushing
**, by crushing
***, 2 by shedding, 31 by crushing; an additional 12 found infected by crushing snails just died (not recorded in table).

TABLE 8. Results of experimentally infecting 5 different groups of snails with the Japanese strain of *Schistosoma japonicum*. A repeat of the experiment documented in Table 7, but with I-lan *Oncomelania hupensis formosana* omitted.

Snails	Experimental				Control	
	No.	Surviving (%)	Infected A (%)	Infected B (%)	No.	Surviving (%)
Oncomelania hupensis hupensis	50	100.0	0	0	10	100.0
O. h. formosana, a	50	94.0	0	0	10	70.0
O. h. formosana, Pu-Yen	50	100.0	0	0	10	100.0
F_1	50	72.0	2.0*	2.78	10	100.0
O. h. nosophora	50	98.0	82.00**	83.7	10	100.0

*, shedding
**, 12% by shedding, 70% by crushing
A, infection in terms of number of snails at the beginning
B, infection in terms of surviving snails

TABLE 9. Results of experimentally infecting 9 groups of snails with the Japanese strain of *Schistosoma japonicum*. Emphasis is on results with F_2 snails.

Snail	Experimental				Control	
	No.	Surviving (%)	Infected A (%)	Infected B (%)	No.	Surviving (%)
Oncomelania hupensis hupensis	50	80.0	2.0	2.5	20	50
O. h. formosana, a	50	58.0	0	0	20	75
O. h. formosana, Pu-Yen	50	94.0	0	0	20	95
F_1	25	64.0	8.0	12.5	10	60
F_2, as	7	100.0	14.0	14.0	0	—
F_2, ar	26	88.5	4.0	4.5	6	83.4
F_2, ps	10	90.0	10.0	11.1	0	—
F_2, pr	50	86.0	2.0	2.3	24	100
O. h. nosophora	50	58.0	36.0*	62.1	20	70

*an additional 14% were infected as found by dissection of snails which had just died.
A, infection in terms of number of snails at the beginning
B, infection in terms of surviving snails
as, albino-smooth
ar, albino-ribbed
ps, pigmented-smooth
pr, pigmented-ribbed

TABLE 10. Summary of the potential for 3 subspecies of *Oncomelania hupensis* to be infected with the Japanese "strain" of *Schistosoma japonicum*.

Investigator	Subspecies	No.	No. miricidia per snail	Snails surviving (%)	Snails Infected A (%)	Snails Infected B (%)
Hunter et al., 1952	*nosophora*	200	1	64.0	6.0	9.4
		135	10	86.6	38.5	44.4
DeWitt, 1954		105	10*	82.9	17.1	20.7
Okamoto, 1963		56	1	>90.0	10.7	27.3
		100?	4	>80.0	22.0?	45.0
		128?	10-20	—	31.3?	83.0
Chi et al., 1971		148	5-7	79.1	26.4	33.3
This paper		180	5	64.5	51.1	79.3
DeWitt, 1954	*hupensis*	64	10*	82.8	28.1	34.0
Chi et al., 1971		82	5-7	69.5	4.9	7.0
This paper		160	5	92.5	1.9	2.0
Hunter et al., 1952	*formosana* (Pu Yen or Changhua)	200	1	97.0	0	0
		135	10	93.3	0.7	0.8
DeWitt, 1954		136	10*	90.4	0	0
Chi et al., 1971		139	5-7	80.6	0	0
This paper		160	5	97.5	0.6	0.6
	(I-lan)					
Moose & Williams, 1964		100	10	89.0	5.0	5.6
This paper		60	5	78.3	0	0
	(Kaohsiung)					
Moose & Williams, 1964		100	10	98.0	0	0
This paper		160	5	75.6	0	0
Chi et al., 1971	*h.* X *f.* (F_1)	110	5-7	78.2	1.8	2.3
This paper		155	5	79.4	2.6	3.3

A, infection in terms of number of snails in the beginning
B, infection in terms of surviving snails
*, 10 miricidia per snail or 15 per pair of snails.

Phenotypes and Susceptibility

It is clear that pigment and ribbing are dominant to albino and smooth. However, it is likewise evident that multiple alleles govern ribbing as there was a gradation in strength of ribs in both F_1 and F_2 generations. We have noted that our breeding stock of *Oncomelania hupensis hupensis* have had some smooth shells in each generation. It is clear that ecological factors alone do not control the presence of ribs as stated by Kuo & Mao (1957). They reported that "...snails bred in moist soil had thin and smooth shells while those bred in water had heavy and coarse shells." This situation should be critically re-investigated.

The transmission of *Schistosoma japonicum* is definitely controlled by the infraspecific genetics of *Oncomelania* and the capacity to transmit is a dominant factor located on a chromosome other than those controlling albinism and ribbing.

The hybrids and F_2 generations could be infected to the same degree as the parental subspecies which was capable of transmitting the Japanese strain of *Schistosoma japonicum* ($1.6 \pm 0.4\%$). The greater percentage of infection in certain F_2 phenotypic classes was correlated with few snails available for infection. It is predicted that the level of infection in all 4 phenotypic classes would be $1.6 \pm 0.4\%$ if the number of snails was 100 or more.

Genes governing the transmission of the Japanese strain of *Schistosoma japonicum* are at a low frequency in *Oncomelania hupensis hupensis* from mainland China and an even smaller frequency in populations of *O. h. formosana* from Taiwan. While the literature generally maintains that Pu Yen, central Taiwanese *O. h. formosana* cannot be infected with the Japanese parasite, the reports of this study show that they can be infected at a 0.6% level. This confirms data from DeWitt (1954) and from similar experiments in Ann Arbor, Michigan in 1964 (Davis, unpubl.) where F_1 generation snails were used. However, although 260 *O. h. formosana* from Kaohsiung (southern Taiwan) have been exposed to the Japanese parasite, none have been infected and genes enabling susceptibility are expected to be found in 0 to 0.3% of these southern populations.

The results of these experiments clearly indicate that several experiments should be conducted when susceptibility phenomena are under investigation. At least 50 snails of each genetic strain should be used in one experiment. At least 150 snails should be used total before conclusive statements can be made about the degree of susceptibility of a population. Note that in one experiment (Table 8), none of the *Oncomelania hupensis hupensis* became infected, while in the course of 3 other experiments 2.0% of the snails were infected.

The optimal number of miricidia to be used is 5 per snail. While one is clearly insufficient, 10 or more overload the system and forced infections may result.

A Model for Studying Genetic Mechanisms of Transmission

Chi *et al.* (1971) have explored the potential of infecting F_1 hybrid snails. If further progress is to be made it is essential to limit studies to 1 or 2 models where in-depth studies are possible. Attention must be focused on results with F_2 snails where genetic reassortment takes place both for phenotypic markers and for susceptibility.

The model presented here is ideal for studying the intramolluscan genetic mechanisms governing the transmission of *Schistosoma japonicum*. Albinism and ribbing are 2 prominent phenotypic markers exploited in this paper; they are not linked with susceptibility. Size and sex are yet other markers; they have not been analyzed here with regard to susceptibility. The problem with size was the eroded apices which made a definitive analysis doubtful. However, improved culture en-

vironment could eliminate the apical erosion problem. Another marker, not analyzed, is the rose-colored shell apex that predominated in our Vogel strain of *Oncomelania hupensis hupensis*. This trait appears to be genetically controlled.

Further study of these snails would undoubtedly reveal further phenotypic markers. The goal is to uncover markers clearly linked to resistance or susceptibility. With such markers one would subsequently work towards isolating the biochemical mechanism which governs susceptibility.

Evolution of *Oncomelania* and Origins of Susceptibility

In recent years considerable attention has been given to the systematics of *Oncomelania* and an understanding of infraspecific taxa relegated to the widespread species *Oncomelania hupensis* (review of Davis, 1971). As stated by Davis (1969, 1971) and Davis & Carney (1973), *Oncomelania* had its origin in an arc from northern Burma to China and spread east along the Yangtze River, finally reaching the southern lowlands. Ribbed morphs are today found concentrated along the Yangtze (see Abbott, 1948, p 264) while smooth morphs are widespread in the southern areas as well as the upper reaches of the Yangtze. When Taiwan became separated from the mainland (about one million years ago) only smooth morphs of *O. hupensis hupensis* were isolated on the island.

The smooth morphs of *Oncomelania hupensis hupensis* on mainland China were previously considered to be *O. h. nosophora* (Abbott, 1948), the subspecies currently restricted to Japan. A thorough understanding of the evolution and spread of *Oncomelania* cannot be possible until numerous populations of smooth and ribbed *O. h. hupensis* from mainland China are compared anatomically and serologically with those from Taiwan and Japan. It has yet to be satisfactorily proven that all the smooth morphs on mainland China are synonymous with *O. h. hupensis* and genetically distinct from I-lan *O. h. formosana* (northeastern Taiwan) and *O. h. nosophora* (Japan).

Oncomelania hupensis hupensis is, with the exception of the isolated *O. h. chiui* of Taiwan, the only subspecies which can transmit all 3 human geographic strains of *Schistosoma japonicum* (Chinese, Japanese, Philippine; see review of Chi *et al.*, 1971). The mainland Chinese strain will not develop in *O. h. nosophora*, *O. h. formosana* or *O. h. quadrasi*. As the geographically isolated snails evolved to their current infraspecific status (*O. h. formosana*, Taiwan; *O. h. chiui*, Taiwan; *O. h. quadrasi*, Philippines; *O. h. nosophora*, Japan; *O. h. hupensis*, mainland China) the parasite evolved with the snail or perished. Genotypes enabling transmission of mainland Chinese *S. japonicum* modified. The fact that *O. h. nosophora* from Japan can transmit the Taiwanese strain of *S. japonicum* but not the mainland Chinese strain suggests closer genetic affinities with *O. h. formosana* (or some smooth as yet unstudied morph of southern mainland Chinese *O. h. hupensis*) than with Yangtze River *O. h. hupensis*. On the other hand, ribbed *O. h. hupensis* have maintained genes enabling transmission of all human strains of *S. japonicum* and thus it is within these populations that the most generalized situation is yet found with regard to mechanisms of transmission of the parasite. Gene frequency enabling transmission of the outlying geographic strains has been reduced by 50 to 60% depending on the geographic human strain (as determined from infectivity studies; see Chi *et al.*, 1971).

Numbers of pertinent questions regarding such genetic relationships can only be answered with future in-depth studies of many mainland Chinese populations of smooth and ribbed *Oncomelania hupensis hupensis*. Careful work with infectivity studies and populations is still very much in need.

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GENETICS OF *BIOMPHALARIA GLABRATA* (GASTROPODA: PLANORBIDAE)

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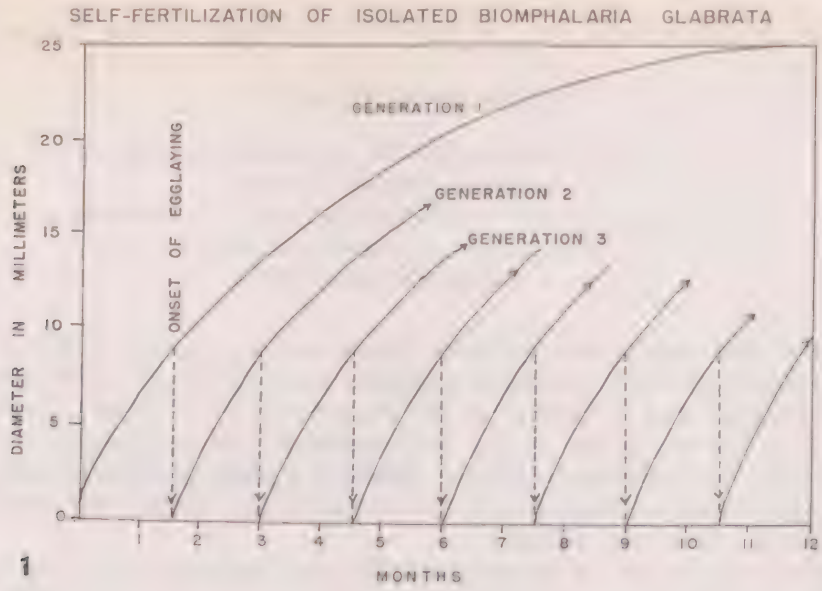
The freshwater pulmonate mollusk *Biomphalaria glabrata* (Say) has been the subject of investigations involving genetics because of its medical importance, and also because of a combination of characteristics uniquely suited to genetic studies. *B. glabrata* is the major intermediate host and vector of *Schistosoma mansoni* in the western hemisphere. Several genetic factors affecting susceptibility of *B. glabrata* to infection with *S. mansoni* have been demonstrated (Richards, 1970; Richards & Merritt, 1972).

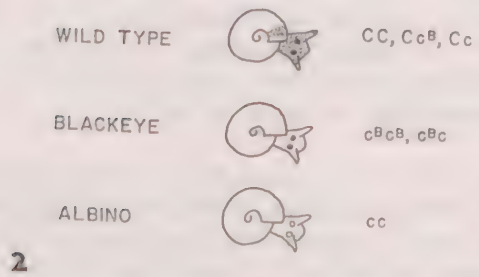
Biomphalaria glabrata is hermaphroditic and isolated snails can reproduce by self-fertilization (Paraense, 1955). Snail stocks can be maintained by selfing through many generations. This facilitates selection for multifactorial genetic characters and identification of new mutations, since even recessive mutants may appear in 1 generation. The generation time in *B. glabrata* (egg to egg) is about 6 weeks under our laboratory conditions, and reproduction may continue for over a year. It is thus potentially feasible to follow 8 consecutive generations in a year (Fig. 1).

When 2 *Biomphalaria glabrata* are mated, by placing them together in the same container, they copulate with each other resulting in reciprocal cross-fertilization. Cross-fertilization dominates, temporarily suppressing selfing (Paraense, 1955). If 2 compatible snails are mated for 1 week, then reisolated, they typically produce 100% cross-fertilized offspring at first, reverting to selfing after about 6 weeks.

Pigmentation serves as a genetic marker in crossing experiments. Newton (1954) showed that albinism in *Biomphalaria glabrata* is a single gene character, recessive to pigmented wild type, and following simple Mendelian inheritance. Another pigment type, "blackeye," appeared as a mutant in 1 of our albino colonies (Richards, 1967). Blackeye is a 3rd allele of the same gene for pigment, being dominant over albino but recessive to wild type pigmentation. We thus have 3 basic pigment phenotypes involving 6 possible genotypes (Fig. 2). An example of the use of pigment as a genetic marker in mating experiments is illustrated in Fig. 3, a cross between a wild type/albino heterozygote and a blackeye/albino heterozygote. Pre-cross selfing of the wild type parent results in wild type and albino offspring in 3:1 ratio; of the blackeye parent in blackeye and albino offspring in 3:1 ratio. Post-cross progeny of both parents include all 3 pigment types in 2:1:1 ratio. Blackeye offspring of the wild type parent and wild type offspring of the blackeye parent can be isolated with the assurance they are the result of cross-cross-fertilization.

The capacity of *Biomphalaria glabrata* for both self-fertilization and cross-fertilization, the short generation time, the long reproductive age span, and the pigment alleles enable us to self an albino and then mate it 4 or more times in succession, alternating wild type and blackeye mates (Fig. 4). The wild type and blackeye mates can, furthermore, then be employed as males in serial crosses with other albinos (Richards & Merritt, 1972) as in Fig. 5. This provides two-





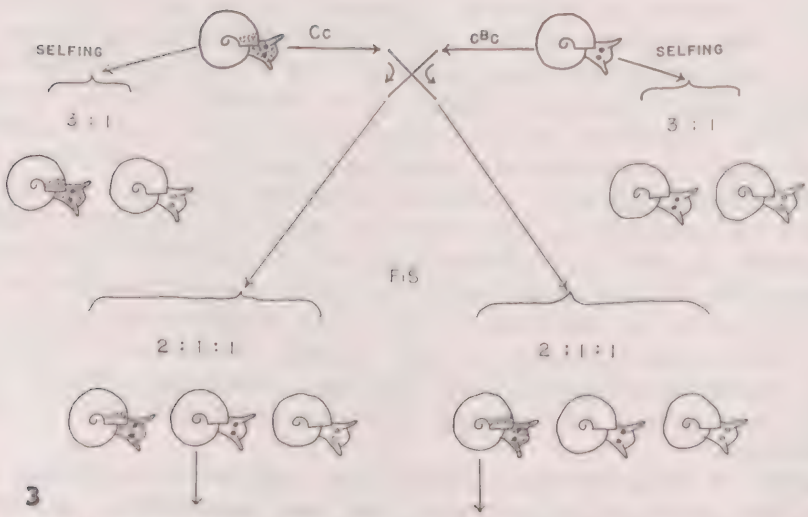
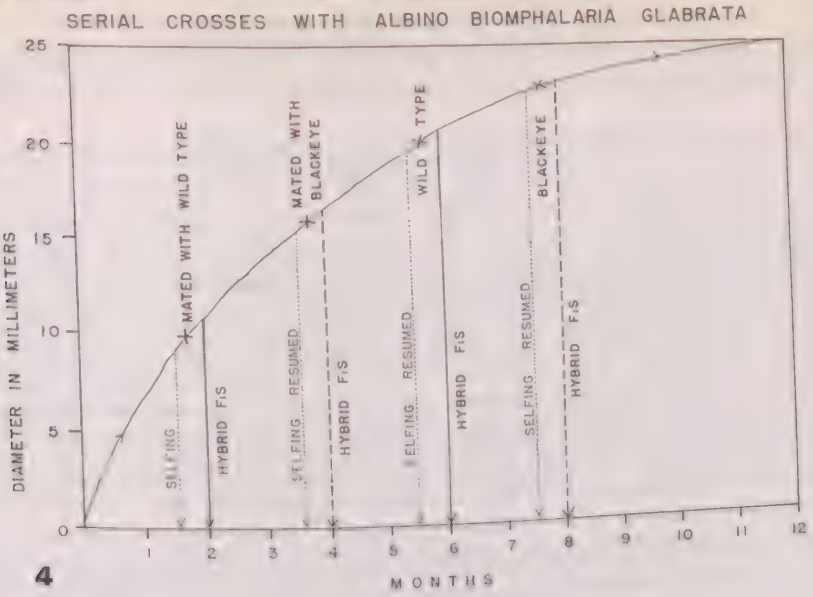


FIG. 1. Successive generations of *Biomphalaria glabrata* by isolated self-fertilization.

FIG. 2. Six possible genotypes and 3 phenotypes for genetic marker pigmentation in *Biomphalaria glabrata*.

FIG. 3. Cross illustrating use of pigment as a genetic marker.



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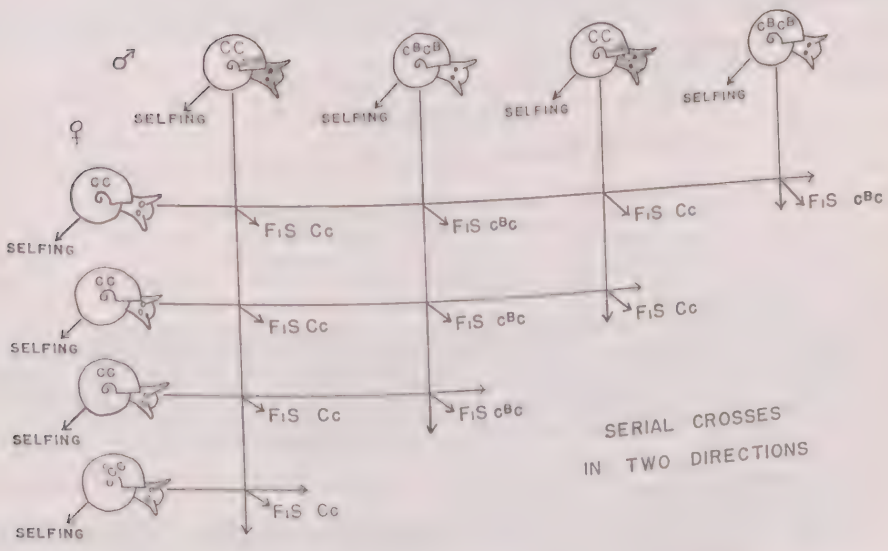

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7 6

FIG. 4. Serial matings of an albino following selfing and alternating wild type and black-eye mates.

FIG. 5. Diagram to illustrate serial crossing in 2 directions.

FIG. 6. Antler tentacle character in *Biomphalaria glabrata*.

FIG. 7. Everted preputium and swollen tentacles character in *Biomphalaria glabrata*.

dimensional genetic comparison, of particular value in analyzing genetic characters which are multifactorial, invisible (such as host-parasite relationships), or both.

Little is known so far about linkage groups in *Biomphalaria glabrata* or other mollusks. Like most of the other species of *Biomphalaria*, *B. glabrata* has 18 pairs of chromosomes (Burch, 1967). Five single gene characters have so far been demonstrated in *B. glabrata*. Crossing experiments suggest that these are inherited independent of each other, thus representing 5 linkage groups. These characters are: (1) basic pigmentation (Fig. 2), (2) pearl formation (a simple recessive; Richards, 1972), (3) antler tentacles (Fig. 6, a simple recessive), (4) everted preputium and swollen tentacles (Fig. 7, a simple recessive) and (5) adult insusceptibility to infection with *Schistosoma mansoni* (Richards, 1970).

In addition to the above, several multifactorial inherited growths have been observed, including pulmonary cavity growths, tentacle and eye variations, and median head bulb (Richards, 1969a, 1970). Other multifactorial genetic characters observed include apertural lamellae (Richards, 1968), spire formation (Richards, 1971), mantle pigment (Richards, 1969b) and susceptibility of juvenile *Biomphalaria glabrata* to infection with *Schistosoma mansoni* (Richards & Merritt, 1972).

Results of investigations to date indicate particularly the importance of gaining further information on the genetics of host-parasite relationships and tumor formation.

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CROSS-BREEDING EXPERIMENTS WITH THE AFRICAN SNAIL GENUS *BULINUS* (GASTROPODA: PLANORBIDAE)[1]

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ABSTRACT

A totally albino strain (i.e., lacking even eye-pigment) of *Bulinus tropicus* (n=18) from Onderstepoort, Transvaal, South Africa was crossed with pigmented snails of each of the following 7 populations: *B. tropicus* (n=18) from Malelane, Transvaal, South Africa; *B. natalensis* (n=18) from Lake Sibayi, Natal, South Africa; *B. tropicus* (n=18) from Lake Baharshangi, Ethiopia; *B. truncatus* (n=36) from Behaira Province, Egypt; *B. sericinus* (n=36) from Toquor River, Ethiopia; *B. hexaploidus* (n=54) from Sulultu River, Ethiopia; *B. octoploidus* (n=72) from Sheno, Ethiopia.

In 2 breeding experiments between the albino *Bulinus tropicus* (n=18) and the pigmented *B. tropicus* (n=18, Transvaal), both albino and pigmented parents produced only eye-pigmented F_1 progeny. The eye-pigmented and albino characters segregated in the expected 3:1 ratio in the F_2 progeny produced by mating F_1 siblings, and in the expected 1:1 ratio when F_1 individuals were backcrossed with albino snails. This indicates that the eye-pigment character is inherited in a simple Mendelian fashion in these populations of *Bulinus*.

In 3 breeding experiments between the albino *Bulinus tropicus* (n=18) and pigmented *B. natalensis* (n=18, Natal), the 3 albino parents produced only pigmented F_1 progeny, demonstrating successful cross-fertilization and dominance of eye-pigment. However, the 3 eye-pigmented parents failed to produce progeny. Here the genetic exchange was in only 1 direction: from pigmented to albino snails. Observation of the F_2 progeny obtained by sibling mating of F_1 snails showed that the eye-pigmented character segregated in the expected 3:1 ratio.

In 4 breeding experiments between the albino *Bulinus tropicus* (n=18) and pigmented *B. tropicus* (n=18, Ethiopia), only 2 albinos produced pigmented F_1 progeny, and these with 25% and 28% embryo mortality. None of the pigmented parents produced eggs. The direction of genetic exchange was in only 1 direction: eye-pigmented to albino snails.

In the above breeding experiments between diploid populations, genetic exchange decreased as geographical separation increased.

In 4 breeding experiments between the albino *Bulinus tropicus* (n=18) and the pigmented *B. truncatus* (n=36, Egypt), neither albino nor pigmented snails produced progeny. In 3 breeding experiments between the albino *B. tropicus* (n=18) and the pigmented *B. sericinus* (n=36, Ethiopia), only 1 pigmented snail produced F_1 progeny: 19 eye-pigmented snails. Sibling mating of F_1 progeny produced no F_2 progeny. However, backcrosses of F_1 progeny to the albino diploid (n=18) snails immediately produced eggs, but with 100% mortality. This indicates that the F_1 progeny were sterile when mated to siblings, but they could at least produce non-developing eggs when backcrossed to albinos.

In 4 breeding experiments between the albino *Bulinus tropicus* (n=18) and the pigmented *B. hexaploidus* (n=54), all 4 pigmented snails produced vigorous pigmented F_1 progeny. However, no F_2 progeny were obtained from the sibling mating of F_1 progeny. In chromosome squash preparations of ovotestes from adult F_1 snails, incomplete meiotic divisions and lack of sperm were observed. None of the albino snails produced eggs. The direction of genetic exchange in these crosses was in only 1 direction: albino to pigmented snails.

In 4 breeding experiments between the albino *Bulinus tropicus* (n=18) and the pigmented *B. octoploidus* (n=72), only 1 pigmented snail succeeded in producing F_1 progeny, which were sterile. A histological study of ovotestes of adult F_1 progeny showed an extremely low number of ova and a lack of sperm. The direction of genetic exchange was again in only 1 direction: albino to pigmented snails.

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MISCELLANEA

MALACOLOGICAL REVIEW - SIX YEARS OF PUBLICATION

Late in 1968 several of us at the University of Michigan discussed the problems of the formal dissemination of scientific information on mollusks, as well as the role of purely malacological journals and their supporting organizations in disseminating this information. From these discussions developed the journal *Malacological Review*, a publication which we hoped would help alleviate several problems in communication between the researcher and the interested potential reader.

Malacological Review has now completed 6 years of publication with this issue of Volume 6 (1973). The journal was initiated in part to complement the function of *Malacologia*, i.e., whereas *Malacologia* was founded to serve mainly as an outlet for longer research papers, *Malacological Review* is better suited to publish shorter papers, including notes and brief communications, as well as announcements and news items of interest to the world-wide malacological community. However, *Malacological Review* may also publish longer papers from time to time, as special needs arise.

Malacological Review was started in Ann Arbor with the assistance of Dr. C. M. Patterson, the cooperation of Drs. C. J. Bayne, S. K. Wu and Mr. J. L. Tottenham, and the overseas affiliation and support (as Participating Editors) of Prof. A. Inaba, (Japan), Prof. R. Natarajan (India) and Dr. W. F. Ponder (Australia). More recently they have been joined by an *ad hoc* group of scientists (Editorial Associates) serving as review editors and including J. N. Cather, E. S. Demian, W. H. Heard, Y. Kondo, G. K. Lindsay and C. T. Lo. Editorial matters regarding illustrations are handled by J. L. Tottenham. Opinions regarding the journal's function are furnished by an Advisory Committee, consisting of Drs. K. J. Boss, J. F. Peake and B. Salvat. Affiliated Editors (editors of other malacological publications affiliated with *Malacological Review*) are K. J. Boss (*Johnsonia* and *Occasional Papers on Mollusks*), A. C. Bruggen (*Basteria*), R. Burn (*Journal of the Malacological Society of Australia*), A. H. Clarke (*Bulletin of the American Malacological Union, Inc.*), D. A. Franchini (*Conchiglie*), A. Girod (*Lavori della Società Malacologica Italiana*), A. Gismann (*Malacologia*), M. A. Klappenbach (*Communicaciones de la Sociedad Malacológica del Uruguay*), R. Krause (*Malakologische Abhandlungen, staatliches Museum für Tierkunde in Dresden*), A. La Rocque (*Sterkiana*), M. K. Mienis (*Argamon*), K. Nicolay (*La Conchiglia*), B. Roth (*The Echo*) and I. Taki (*Venus*).

Inasmuch as there are now some 18 malacological journals from 10 countries actively publishing, as well as 2 international malacological journals, the need for an instrument to centralize this important literature is clearly evident. Since current subscriptions and complete sets of the malacological journals are available in only a few institutions, usually only 1 or 2 in each of the more industrially developed nations, it is important for the many malacological researchers who do not have access to these resources to know what is being published, where and by whom. To this end, *Malacological Review* has been publishing the tables of contents of all the malacological journals, beginning with the year 1967. Also included with this coverage is a list of addresses of the authors publishing in these journals. The latter is intended for those who wish to write to authors for separates or reprints of their papers. Additionally, *Malacological Review* will from time to time publish the tables of contents of relevant mollusk publications that may not come strictly under the classification of "journal," such as *Leaflets in Malacology*, or especially obscure "journals" such as *Gastropodia* (e.g., see *Malacological Review*, 5(1): 28-34).

Malacological organizations affiliated with *Malacological Review* are the Malacological Society of Australia, the Malacological Society of Japan, the Nederlandse

Malacologische Vereniging, the Sociedad Malacológica del Uruguay, the Società Malacologica Italiana, the Société Belge de Malacologie, the Society for Experimental and Descriptive Malacology, the Israel Malacological Society, the Unione Malacologica Italiana, the Unitas Malacologica Europaea and the Western Society of Malacologists.

The group which sponsors and directs *Malacological Review* was formed in September 1968 and incorporated under the laws of the state of Michigan as the Society for Experimental and Descriptive Malacology in December 1970. Officers in this organization are J. B. Burch, C. M. Patterson and G. K. Lindsay. This Society, in addition to publishing the journal, has also sponsored 3 annual Mollusk Seminars in Ann Arbor.

Malacological Review was first published in 1 number for the year 1968. This single issue (187 pages) constituted Volume 1. During each of the years 1969, 1970, 1971, 1972 and 1973 (Vols. 2, 3, 4, 5 and 6, respectively) 2 semiannual numbers were published, each 2 issues for a calendar year constituting a volume. Hereafter we intend to continue publishing 2 issues a year, each formally designated as a "number." The first issue of each volume henceforth will be "Vol. ___, No. 1" and the second issue "Vol. ___, No. 2." Occasionally, both issues for a calendar year may be combined and designated as "Vol. ___, No. 1-2." Each volume will normally consist of about 200 pages, although this may vary from time to time.

Publication dates of past issues are as follows: Vol. 1, 7 June 1969; Vol. 2 [No. 1], pages 1-102, 10 June 1969; Vol. 2 [No. 2], pages 103-214, 8 May 1970; Vol. 3 [No. 1], pages 1-102, 28 May 1970; Vol. 3 [No. 2], pages 103-192, 13 March 1971; Vol. 4, No. 1, 27 July 1971; Vol. 4, No. 2, 10 February 1972; Vol. 5, No. 1, 31 July 1972; Vol. 5, No. 2, 12 January 1973; Vol. 6, No. 1, 12 April 1973.

Sixty-seven authors have contributed scientific papers to the first 6 volumes of *Malacological Review*, representing the following 13 countries: Australia, Canada, France, Hong Kong, India, Israel, Japan, Liberia, the Netherlands, New Zealand, South Africa, U.S.A. and U.S.S.R.

Malacological Review has published 5 review articles, 31 research articles, 19 brief scientific communications, 13 book reviews, 5 obituaries, 8 contributions under "Miscellanea," 48 abstracts of scientific papers (46 in the *Proceedings* of the Society for Experimental and Descriptive Malacology and 2 in the American Malacological Union Symposium, "Genetics, cytogenetics and hybridization of mollusks"), 76 notices and announcements, and 1,039 entries in the "Publications" sections. The average length of the review papers was 13 pages and the average length of the research papers was 19 pages. Areas of research dealt with in articles published to date include behavior, biochemistry, comparative and descriptive morphology, conchology, conchometry, conservation, culture methods, cytogenetics, cytotaxonomy, defense mechanisms, development, ecology, electrophoresis, evolution, feeding, functional morphology, genetics, growth, histochemistry, historical biology, hybridization, immuno-taxonomy, natural history, organ culture, paleontology, parasites and parasitism, phylogeny, physiology, systematics, techniques, variation, zoogeography and distribution, and zoological nomenclature.

Malacological Review has published on 3 occasions the *Proceedings* of the Society for Experimental and Descriptive Malacology (in Vol. 2, No. 1; Vol. 5, No. 1; and Vol. 6, No. 1) and will publish the 4th *Proceedings* in Vol. 7. The journal also published (in Vol. 6, No. 2) the contributions to the 1972 American Malacological Union's symposium on "Genetics, cytogenetics and hybridization of mollusks."

Malacological Review has published 1 supplement, *"Freshwater snails of Taiwan (Formosa)"* by Gary L. Pace. This publication of 118 pages is not included in the regular subscription price of the journal. Its price is US$ 15.00. *Malacological Review* had earlier planned to publish another supplement, but later decided against it.

Articles in *Malacological Review* have been published in English, French and German. The great majority of the papers have been in English.

Information on subscriptions for the 1st 6 years is summarized in the table below.

Country	Private Individuals	Institutions	Total
Algeria	1	1	2
Argentina	3	3	6
Australia	15	12	27
Austria	2	1	3
Belgium	5	4	9
Brasil	5	8	13
Canada	18	25	43
Canal Zone	1	0	1
Chile	0	1	1
China (Nationalist)	1	1	2
Cuba	0	1	1
Denmark	1	1	2
Egypt	3	0	3
Finland	0	1	1
France	7	21	28
Germany (D. R.)	0	1	1
Germany (F. R.)	12	6	18
Ghana	0	1	1
Hungary	2	0	2
India	2	7	9
Indonesia	0	2	2
Iran	0	2	2
Ireland (Eire)	0	1	1
Israel	1	4	5
Italy	8	8	16
Japan	15	8	23
Korea	3	1	4
Malagasy	0	1	1
Mexico	3	0	3
Monaco	0	1	1
Netherlands	6	4	10
New Caledonia	1	0	1
New Zealand	1	8	9
Norway	0	4	4
Philippines	0	1	1
Poland	0	2	2
Portugal	2	1	3
South Africa	1	10	11
Spain	5	1	6
Sweden	0	2	2
Switzerland	2	3	5
Thailand	0	1	1
Uruguay	0	1	1
U. K.	6	21	27
U. S. A.	229	144	373
U. S. S. R.	1	3	4
Venezuela	1	1	2
West Indies	5	0	5
Yugoslavia	1	2	3
	369	332	701

Portrayed on the covers of *Malacological Review* are a series of mollusk shells, a different set with a different color background on each volume. Those on Vol. 1 are Succineidae (brown shells on tan background with green lettering), on Vol. 2 are species of the lymnaeid genus *Stagnicola* (dark grey on tan background with maroon lettering), on Vol. 3 are Epitoniidae (dark blue on light blue background with gold lettering), on Vol. 5 are species of the unionacean genus *Dysnomia* (dark green on light green background with purple lettering) and on Vol. 6 are various gastropod species occurring in the Lake Ohrid region, Macedonia, Yugoslavia [species of *Acroloxus*, *Ancylus*, *Ginaia*, *Gyraulus*, *Hippeutis*, *Planorbis*, *Pyrgula* and *Radix*] (grey on yellow background with black lettering). John L. Tottenham drew the shells on Vols. 1-5 and Carole W. Christman drew those on Vol. 6. The shells on the 2nd number of each volume (except for Vol. 1 which was completed in 1 issue) are simply outlines of the shells appearing on the 1st number of the volume, and although color background is the same as the preceding number of the particular volume, the ink for the shells and lettering is black.

Subscription price for *Malacological Review* is US$ 5.00 (postpaid) for private individuals residing in the U.S.A. and US$ 5.50 for private subscribers in all other countries. Subscription price for institutions is US$ 8.00 and US$ 9.00 for all orders placed through North American subscription agencies or for orders paid by UNESCO coupons.

J. B. BURCH

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NEWS AND ANNOUNCEMENTS

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THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND, PROGRAM OF MEETINGS FOR 1973. – The meetings of the Conchological Society are held in The Conversazione Room, British Museum (Natural History), Cromwell Road, South Kensington, S.W. 7, England, U.K. at 2:30 p.m. The program of subjects for exhibition and discussion is as follows:

"Mollusks of the Trucial Coast" — Exhibition, January 20, 1973.
"Collecting and photographing shells of the Trucial Coast," by Mrs. K. R. Smythe, January 20, 1973.
Open exhibition — Annual General Meeting, February 24, 1973.
"Fictional Mollusca," by T. E. Crowley, Presidential Address, February 24, 1973.
"Marine bivalves" — Exhibition, March 17, 1973.
"The oyster in literature," by A. E. Ellis, March 17, 1973.
"British land Mollusca" — Exhibition, April 14, 1973.
"Researches on the land snail *Cepaea nemoralis*," by A. J. Cain, April 14, 1973.
"Parasitology" — Exhibition, May 19, 1973.
"*Lymnaea truncatula*, the snail host of the liver fluke," by C. B. Ollerenshaw, May 19, 1973.
"Biological recording" — Exhibition, October 20, 1973.
"Mapping the fauna of Europe," by J. Heath, October 20, 1973.
"Pleistocene fossils" — Exhibition, November 17, 1973.
"Post glacial history of British land molluscs," by M. P. Kerney, November 17, 1973.
"Photographic records" — Exhibition, December 15, 1973.
"Field meeting reminiscences," by J. Llewellyn Jones, December 15, 1973.

The Honorable Secretary of the Society is Mrs. E. B. Rands, 51 Wychwood Avenue, Luton, Beds. LU2 7HT, England, U.K.

MALACOLOGICAL SYMPOSIUM, AUSTRALIA. – A Malacological Symposium was held at the University of Queensland Marine Station at Dunwich, Queensland, Australia, 16-21 June 1973.

The symposium, sponsored by The Australian Museum, Sydney, was attended by 28 people, including the local committee (Dr. Winston F. Ponder, Helen Williams King, Mr. & Mrs. Philip H. Coleman, Mr. E. K. Yoo and Ms. Colleen Robinson).

Program

Micro-molluscan distribution patterns in the Hawaiian Islands and at Fanning Island. A. KAY, *University of Hawaii*.
Australian paryphantids. B. J. SMITH, *National Museum of Victoria*.
Taxonomy of *Tutufa* and related Bursidae. A. G. BEU, *New Zealand Geological Survey*.
Mollusks and medicine in Australia. J. WALKER, *University of Sydney*.
Comments on man-distributed molluscs in Pacific Islands. H. HARRY, *Agricultural and Mechanical University of Texas*.
Tertiary Volutidae of southeastern Australia. T. DARRAGH, *National Museum of Victoria*.
Ecology and reproduction of sub-antarctic littoral mollusks. R. SIMPSON, *University of New England*.
Molluscs parasitic on echinoderms in Japan. T. HABE, *National Science Museum (Tokyo)*.
The relationships and evolution of the Neogastropoda. W. F. PONDER, *The Australian Museum*.
Origin and evolution of the Australian Trigoniidae. T. DARRAGH, *National Museum of Victoria*.
Character weighing in pulmonates. A. SOLEM, *Field Museum of Natural History (Chicago)*.
Pacific Partulidae. J. B. BURCH, *The University of Michigan*.
The classification of North Pacific Buccinidae. T. HABE, *National Science Museum (Tokyo)*.
Rediscovery of *Clavagella lata*. B. J. SMITH, *National Museum of Victoria*.
Stratigraphic hazards and Tertiary molluscan taxonomy in southern Australia. N. LUDBROOK, *Geological Survey of South Australia* (ret.).
The prosobranch veliger. V. FRETTER, *University of Reading*.
Non-marine mollusc survey of Victoria. B. J. SMITH, *National Museum of Victoria*.
Species recognition in land snails. B. L. GIRARDI, *Field Museum of Natural History*.
Thoughts on the classification of the Mytilidae. B. R. WILSON, *Western Australian Museum*.

Special Seminars

New methods in molluscan taxonomy and their relationship to classical taxonomic practice. Chaired by J. B. BURCH
Collecting and conservation - is there need for restrictions? Chaired by A. KAY
The role of museums and their collections; immediate problems and the best use of available resources. Chaired by B. J. SMITH

Zoogeography in the Indo-Pacific - terrestrial and marine. Chaired by A. SOLEM
Current state of Australian and Indo-Pacific molluscan taxonomy, ecology and biology. Some ideas for the future. Chaired by B. R. WILSON

Malacologists attending the Symposium. Left to right, 1st row: Harold Rehder, Colleen Robinson, Marjorie Colman, Nellie Ludbrook, Tadashige Habe, Philip Colman, Vera Fretter, Shirley Slack-Smith. Second row: E. K. Yoo, Joan Beu, Harold Harry, Alan Beu, Alison Kay, Helen Williams King, Lois Rehder. Back rows: Betty Lou Girardi, Winston F. Ponder, Ronald Simpson, John Walker, Thomas Darragh, Alan Solem, M. Buonaiuto, Brian Smith, Millicent Harry, Frank Climo, Barry Wilson, J. B. Burch.

AMERICAN MALACOLOGICAL UNION, 39th ANNUAL MEETING. — This meeting, held June 25-29, 1973, was hosted by the University of Delaware and the Delaware Museum of Natural History. It was well attended by the second largest group in the history of the organization. Dr. Tucker Abbott was the official host. Most activities were held at the Clayton Convention Center at the University of Delaware, although one day was devoted to sessions held at the Delaware Museum of Natural History. President D. S. Dundee had various AMU members presiding at the several sessions, where 32 papers were presented. Two symposia were also given: "Specimen Photography," organized and conducted by Mr. Dan Steger and Mr. Robert Lipe; and "What is a species? a subspecies?", organized by Dr. Harold Murray and with J. P. E. Morrison, D. H. Stansbery, G. M. Davis, K. J. Boss, R. T. Abbott and M. K. Jacobson as participants. A field trip to Cape Henolopen National Park allowed for collecting and, on the same trip, a visit to the Mariculture Experimental Project gave malacologists an opportunity to see the latest in marine aquaculture.

MOLLUSK SEMINAR, ANN ARBOR, AUGUST 1972. — A seminar on mollusks was held at The University of Michigan, Ann Arbor, on 24 and 25 August 1973. The 21 papers presented at the seminar are listed below.

Program

Opening remarks, J. B. BURCH

Systematics, Variation and Zoogeography

Convener, James N. CATHER

A review of the *Lampsilis radiata* (Gmelin, 1791) complex in North America (Mollusca: Bivalvia: Unionidae). David H. STANSBERY
Anatomical systematics of freshwater mussels. William H. HEARD
Comparative reproduction in viviparid snails. Virginia VALE
Studies on Physidae (Pulmonata: Basommatophora). George A. TE

Scanning electron microscope studies of the embryonic shell surface sculpture in *Bulinus*. C. M. PATTERSON
Freshwater mollusks of Lake Ohrid, Macedonia. S. HADŽIŠČE, J. B. BURCH and C. M. PATTERSON

Growth, Development, Behavior, Physiology and Biochemistry

Convener, C. M. PATTERSON

Effects of various kinds of algae, aquaria, muds and mud extracts, and synthetic muds on the growth of *Biomphalaria pfeifferi*. Y. S. LIANG
Life table parameters of an experimental population of *Omalonyx felina* (Pulmonata: Succineidae). Amy L. SHRADER
Embryological development in *Dentalium*. James N. CATHER
The structure, ciliation and function of the lips of bivalves. T. H. J. GILMOUR
Structure of calcareous snail eggs. Alex S. TOMPA
Behavior responses of *Biomphalaria glabrata*. William A. SODEMAN
Behavioral and physiological studies on locomotion in the giant garden slug, *Limax maximus*. David J. PRIOR
Comparative aspects of the morphology and physiology of a single identified neuron in several stylommatophoran snails. David SENSEMAN
The histochemical identification of galactogen in the Succineidae. Paul H. RUDOLPH
Organ culture of *Helix pomatia* albumen gland in a defined medium. Shelley L. FELDMAN and Esther M. GOUDSMIT

Snails as Intermediate Hosts of Parasites

Convener, William H. HEARD

A simple biochemical method for discerning between diploid and polyploid species of the *Bulinus* (*Isidora*) complex. G. K. LINDSAY
The genus *Bulinus* and schistosomiasis in North Africa. Philip T. LoVERDE
Biology and control of *Bulinus truncatus*. Emile S. DEMIAN
Experimental infection of *Bulinus sericinus* with *Schistosoma haematobium*. S. K. WU and J. B. BURCH
The antagonistic action of *Paragonimus ohirai* and *Schistosoma japonicum* in *Oncomelania nosophora*. Philip T. LoVERDE and Marilyn PARKER

THE FIRST ASIAN MALACOLOGICAL SYMPOSIUM, HONG KONG. — This symposium is to be organized by Dr. B. S. Morton to provide an opportunity for malacologists interested in the Indo-Pacific area to meet in Hong Kong in conjunction with the Marine Sciences Symposium (December 7-16, 1973). Provisional plans are for the malacological symposium to be held at the Department of Zoology, The University of Hong Kong on December 17 and 18, 1973.

A COLLOQUIUM ON MOLLUSCAN PHYLOGENY, LONDON. — This colloquium is sponsored by The Palaeontological Association and is to be held on April 3 and 4, 1974, at Bedford College, Regents Park, London, England. It is intended to be an informal residential "workshop" bringing together zoologists and palaeontologists to discuss common problems of molluscan relationships. The colloquium will be arranged as a series of sessions devoted to the origin of the Mollusca, the radiation of molluscan classes and the relationships and evolution within the bivalves, gastropods, cephalopods and other classes. Other topics may include the evolution of locomotion and skeletal organisation within the phylum. Each session will be introduced by a general review from both zoological and palaeontological viewpoints and then followed by open ended discussion. Accommodation will be arranged at Hanover Lodge, Regent's Park (8 minutes walk from Bedford College) from the evening of April 2 until the morning of April 5. Enquiries and further information can be obtained from N. J. Morris or J. D. Taylor, British Museum (Natural History), Cromwell Road, London SW7 5BD, England, U.K.

SUPPLEMENT 1, *MALACOLOGICAL REVIEW — FRESHWATER SNAILS OF TAIWAN (FORMOSA)*. — *Malacological Review* has published its Supplement No. 1, *Freshwater snails of Taiwan* (*Formosa*), by Gary L. Pace. This illustrated publication deals with the systematics, ecology, distribution, zoogeography and parasitological relationships of the freshwater gastropod fauna of Taiwan, The Republic of China. The price of this monograph (US$ 15.00) is not included in the regular subscription price to *Malacological Review*, but can be purchased upon order from our American, Australian or Japanese editorial offices (see inside back cover for addresses).

MALACOLOGICAL REVIEW, P.O. Box 801, Whitmore Lake, Michigan 48189, U.S.A.

BOOK REVIEWS

THE MOLLUSKS OF THE ARID SOUTHWEST WITH AN ARIZONA CHECKLIST. Joseph C. Bequaert & Walter B. Miller. The University of Arizona Press, Box 3398, Tucson, Arizona 85722, U.S.A. p i-xvi, 1-271.

This is one of the few significant publications on North American land snails since H. A. Pilsbry's (1939-48) *Land Mollusca of North America*. Bequaert & Miller's *The Mollusks of the Arid Southwest with an Arizona checklist* consists of 2 sections, the first a discussion entitled "Zoogeography of southwestern Nearctic mollusks" and the second an "Annotated checklist of Recent Arizona mollusks."

In introducing the zoogeography section, the authors clearly define the boundaries of the Nearctic southwestern molluscan province as well as provide definitions for the terminology used in their discussion. A detailed distribution in the Nearctic southwestern molluscan province is given for the 6 major genera (2/3 of the total number of land snail species - *Ashmunella*, *Eremarionta*, *Holospira*, *Humboldtiana*, *Oreohelix* and *Sonorella*) with an accompanying map which shows the distributional boundaries. The distribution of the "lesser" land mollusks (snails), many of which are minute species, is also given, but without accompanying maps. Other points are often included in the zoogeographical discussion of the genera. For example, the authors may speculate on the ancestry and mechanism of speciation in a genus, present some distinctive morphological features of the genus and, in other cases, mention information available from the fossil record. The zoogeography section is concluded with a discussion on "terrestrial mollusks and the arid environment," including a comparison of the North American southwestern land snail fauna with data on the faunas inhabiting arid lands in southwest Africa. The obvious and perhaps remarkable evolutionary trends show that speciation has been enhanced (or stimulated) by the extreme conditions of the arid environment. In fact, the authors point out that there is evidence for a continuing active evolution at present for the large princinctive land snails inhabiting the Southwestern province.

Their zoogeographical account, although somewhat limited by older concepts of biogeography, is presented in an authorative, straightforward and well organized manner. It seems clear that firsthand field studies combined with years of detailed study of these Southwestern province land snails has given the authors a clear concept of apparent evolutionary trends in these genera.

In the second part, the annotated checklist of Recent Arizona mollusks, the authors treat both land and freshwater mollusks (including pelecypods) and provide collection records and precise distribution in Arizona for the various species, as well as presenting the generalized occurrence in other parts of North America. In some cases the authors clarify records based on mis-identifications and present synonymies of some of the species. Their treatment of the large land snail species is most thorough. The Succineidae posed problems for the authors since precise identification must be based on anatomical features and often they had only shells available. However, they do recognize 5 species in Arizona. One of these they call *Succinea* (*Novisuccinea*) *avara*. This name cannot be applied to any succineid with certainty as pointed out by Hubricht (1958, *Nautilus*, 72: 60-61). Furthermore, *Novisuccinea* is not a valid subgenus (Patterson, 1971, *Malacol. Rev.*, 4(1): 131-202).

Although the authors have spent most of their time on land snails, nevertheless their treatment of the freshwater mollusks is generally quite careful. The cover-

age of the Lymnaeidae is good and the nomenclature and taxonomic groupings basically follow current concepts of the more active lymnaeid specialists. However, it should be pointed out that *"Stagnicola" (Bakerilymnaea) bulimoides techella* (Haldeman), as well as the type species of *Bakerilymnaea*, Pfeiffer's (1839) *"Limnaea cubensis,"* have now been shown to belong to *Fossaria* (see Burch & Lindsay, 1972, *Malacol. Rev.*, 5(1): 16-17; LoVerde & Burch, 1973, *Malacol. Rev.*, 6(1): 44) rather than to *Stagnicola*, the genus to which the authors assign the species. In the family Physidae, the assignment of *Physa virgata* and *P. humerosa* to the subgenus *Physella* is still open to question since such a decision must be based on information from anatomical studies. A serious lapse in nomenclature is in the handling of the Ancylidae. *Ferrissia* should not be used as a subgenus of *Laevapex*. Basch (1959, *Misc. Publs. Mus. Zool., Univ. Mich.*, No. 108: 1-56) has shown that the 2 groups are quite distinct. Additional differences are discussed by Burch (1962, *Malacologia*, 1(1): 55-72; 1962, *Amer. malacol. Union, ann. Reps.*, 29: 8-9). Similarly, Haldeman's (1841) *Ancylus parallelus* belongs to *Ferrissia* and not to *Laevapex*, the genus to which the authors assign the species.

Following the annotated checklist is a useful and rather complete bibliography. Like any such compilation which covers a vast area of literature, there have been some important omissions (mostly in dealing with freshwater gastropods). A more serious omission is the virtual lack of illustrations for any of the mollusks discussed, an omission which limits the usefulness of the book. It would seem that at least photographs of shells could have been provided. Thus, the book is strictly for the specialist who can readily recognize all the species dealt with.

Generally the book is well written and seems to accomplish what the authors intended. The authors have taken care and exercised caution in dealing with mollusk groups with which they are not so familiar or which have been little studied by malacologists. This book will certainly be a valuable addition to the professional malacologist's library, although it is probably of only limited value to the non-malacologist or amateur.

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[2]Prominent shell collectors' magazines may be included in future numbers of *Malacological Review*.
[3]Footnotes 4–23 list the main editorial offices of the various journals.
[4]18/55 Prince Albert St., Mosman, N.S.W. 2088, Australia.
[5]Senckenbergishchen Naturforeschende Gesellschaft, Senckenberg-Anlage 25, 6 Frankfurt 1, Germany (FR).
[6]The Nook, Uplands Rd., Bromborough, Cheshire, U.K.
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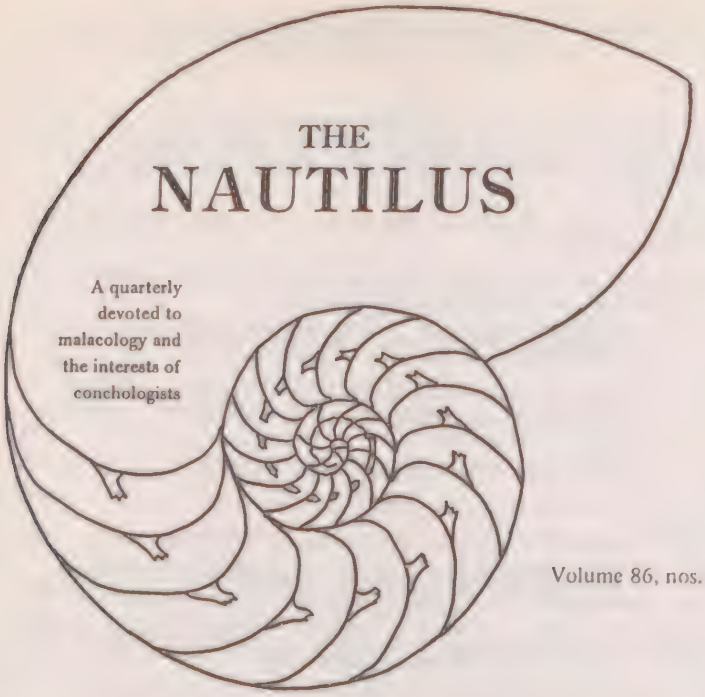

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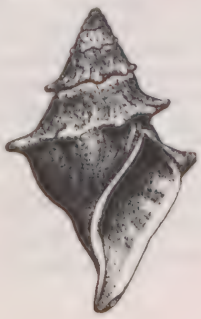

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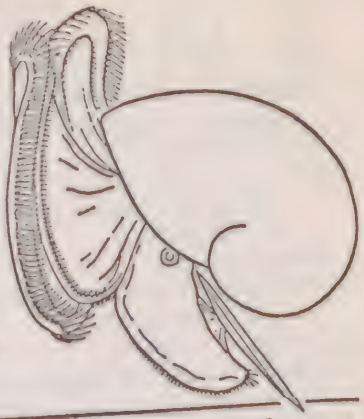

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June 18-21, 1972

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OF THE

FIFTH ANNUAL MEETING

OF

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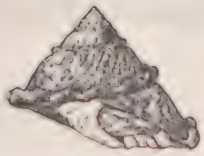

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